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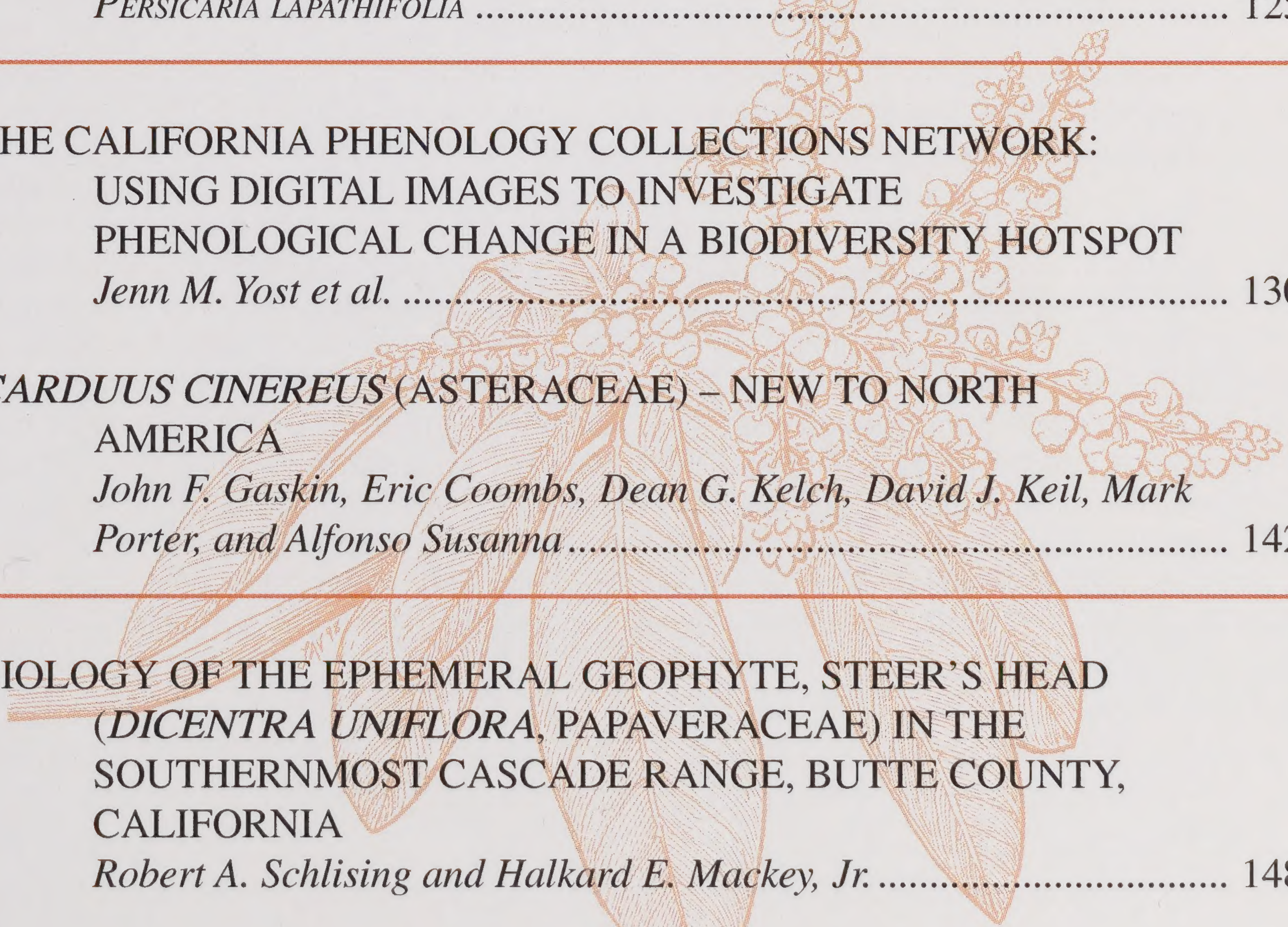

NOTEWORTHY COLLECTIONS

ALASKA
Carex echinata, Carex lapponica, Carex phaeocephala, Draba aleutica, Eriophorum viridicarinatum, Limosella aquatica, Primula tschuktschorum, Gnaphalium uliginosum, Phleum pratense and *Persicaria lapathifolia* 125

NOTES

THE CALIFORNIA PHENOLOGY COLLECTIONS NETWORK: USING DIGITAL IMAGES TO INVESTIGATE PHENOLOGICAL CHANGE IN A BIODIVERSITY HOTSPOT
Jenn M. Yost et al. 130

CARDUUS CINEREUS (ASTERACEAE) – NEW TO NORTH AMERICA
John F. Gaskin, Eric Coombs, Dean G. Kelch, David J. Keil, Mark Porter, and Alfonso Susanna 142

CONTENTS

BIOLOGY OF THE EPHEMERAL GEOPHYTE, STEER'S HEAD (*DICENTRA UNIFLORA*, PAPAVERACEAE) IN THE SOUTHERNMOST CASCADE RANGE, BUTTE COUNTY, CALIFORNIA
Robert A. Schlising and Halkard E. Mackey, Jr. 148

TREE MORTALITY IN BLUE OAK WOODLAND DURING EXTREME DROUGHT IN SEQUOIA NATIONAL PARK, CALIFORNIA
Adrian J. Das, Nicholas J. Ampersee, Anne H. Pfaff, Nathan L. Stephenson, Tedmond J. Swiecki, Elizabeth A. Bernhardt, Patricia K. Haggerty, and Koren R. Nydick 164

NEW SPECIES

SILENE NELSONII, A NEW LARGE-FLOWERED SPECIES FROM THE TRINITY RIVER AREA OF NORTHWESTERN CALIFORNIA, USA, AND A RE-EVALUATION OF *S. BOLANDERI* GRAY
Michael R. Mesler, Michael S. Mayer, and Sydney K. Carothers 176

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Editor—JUSTEN B. WHITTALL
Department of Biology
Santa Clara University
500 El Camino Real
Santa Clara, CA 95053
madronoeditor@gmail.com

Book Editor—MATT RITTER
Noteworthy Collections Editor—DAVID KEIL
Copy Editor—ALISA HOVE

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California Botanical Society
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1001 Valley Life Sciences Building
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NOTEWORTHY COLLECTION

ALASKA

CAREX ECHINATA Murr. subsp. *ECHINATA* (CYPERACEAE). Lake and Peninsula Borough, Katmai National Park and Preserve (KATM), Kukak Bay, 58.34°, -154.18° (WGS84; detailed coordinates withheld, taxon is on Alaska rare plant list), 32 m, 15 July 2017, *M. J. Macander with T. Christopherson, S. L. Ives, and A. F. Wells* (ALA V177883). Uncommon in a wetland on a small coastal peninsula, growing on organic soils (pH 5.9) with *Calamagrostis canadensis* (Michx.) P.Beauv., *Carex lyngbyei* Hornem., *Carex tenuiflora* Wahlenb., *Equisetum fluviatile* L., and *Eriophorum viridicarinatum* (Engelm.) Fernald.

Previous knowledge. *Carex echinata* subsp. *echinata* has an Alaska state rare ranking of S1S2 and a global rare ranking of G5T5 (ACCS 2019). A state ranking of S1S2 means this subspecies is considered critically imperiled to imperiled within Alaska and is at risk of extirpation because of very few occurrences and limited range extent. A global ranking of G5T5 means this subspecies is considered secure (common, widespread, and abundant) globally. This taxon is widespread elsewhere in North America; it occurs in eight Canadian provinces; and in 35 U.S. states (Ball and Reznicek 2003). Outside of North America, this species is known from Eurasia. There are 11 previous records of this subspecies in Alaska. Four records come from the Skwentna River drainage in south-central Alaska, one from the eastern Alaska Range near the community of Paxon, four from the Aleutian Islands (Unalaska Island), and two from the central Alaska Range in Denali National Park and Preserve (Roland 2004; ACCS 2019; ARCTOS 2019; CPNWH 2019; IRMA 2019). See Carlson et al. (2013) for additional discussion of this taxon in southwestern Alaska and Carlson and Heitz (2018) for floristic patterns in southwestern Alaska.

Significance. This is the first record of subsp. *echinata* on the Alaska Peninsula and in KATM.

CAREX LAPPONICA O.F.Lang (CYPERACEAE). Lake and Peninsula Borough, KATM, Douglas River valley, 58.87°, -153.86° (WGS84; detailed coordinates withheld, taxon is on Alaska rare plant list), 91 m, 13 July 2017, *S. L. Ives with A. F. Wells* (ALA V177884). Common in a beaver dam wetland complex; soils wet, silty clay loam over loamy very fine sand (pH 6.1), growing with *Arctophila fulva* (Trin.) Anderss., *Carex canescens* L., *Carex utriculata* F.Boott, and *Juncus filiformis* L.

Previous knowledge. *Carex lapponica* has an Alaska state rare ranking of S3S4 and a global rare ranking of G4G5 (ACCS 2019). A state ranking of S3S4 means this species is rare to apparently secure, but uncommon within the state. A global ranking of G4G5 means this species is apparently secure globally. This taxon is known to occur in North America in seven Canadian provinces, and in the U.S. only in Alaska. Outside of North America, this species is known from northern Eurasia (Ball and Reznicek 2003). There are 33 previous records of this species in the state (ACCS 2019; ARCTOS 2019; CPNWH 2019). Records of this species are widely scattered in Alaska south of the Brooks Range, excluding the Aleutian Island and the Alexander Archipelago. Previous accounts of this species on National Parklands in Alaska include: Denali National Park and Preserve (Roland 2004), Yukon-Charley Rivers National Preserve (Roland et al. 2004), Gates of the Arctic National Park and Preserve and Kobuk Valley National Park (Parker 2006), and Wrangell-St. Elias National Park and Preserve (Cook et al. 2007).

Significance. This is the first record of this rare species on the Alaska Peninsula, and the first record in KATM.

CAREX PHAEOCEPHALA Piper (Cyperaceae). Lake and Peninsula Borough, KATM, near the foot of Hallo Glacier, 58.41°, -154.17° (WGS84; detailed coordinates withheld, taxon is on Alaska rare plant list), 43 m, 16 July 2017, *S. L. Ives with A. F. Wells* (NPS Museum Collection KATM-00652 Cat. #55024). Uncommon on partially vegetated, recently deglaciated, glaciofluvial deposits; soils dry, extremely gravelly sand over fine sand (pH 7.1). Growing with *Alnus viridis* ssp. *sinuata* (Regel) A.Löve & D.Löve, *Poa arctica* R.Br., *Racomitrium ericoides* (Web. ex Brid.) Brid., *Salix alaxensis* (Andersson) Coville, and *S. sitchensis* Sanson ex Bong.

Previous knowledge. *Carex phaeocephala* has an Alaska state rare ranking of S3 and global rare ranking of G4 (ACCS 2019). A state ranking of S3 means this species is rare in Alaska and at moderate risk of extirpation. A global rare ranking of G4 means this species is secure, but uncommon globally, and there is some cause for long-term concern. This taxon is known to occur in North America in three western Canadian provinces and 10 U.S. states (Ball and Reznicek 2003; CPNWH 2019). There are 36 previous records of this species in Alaska (ACCS 2019; ARCTOS 2019; CPNWH 2019). Records are concentrated in rocky alpine and deglaciated habitats in the Chugach, Kenai, St. Elias, and western Alaska Range, the Aleutian Range mountains, and mountains of southeast Alaska. Previous accounts of this species on National Parklands in Alaska include: Denali National Park and Preserve (Roland 2004),

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Wrangell-St. Elias National Park and Preserve (Cook et al. 2007), and Kenai Fjords National Park (Carlson et al. 2004a, 2013).

Significance. This is the furthest southwest record of this species in Alaska, and the first record in KATM.

DRABA ALEUTICA Ekman (BRASSICACEAE). Lake and Peninsula Borough, KATM, Aleutian Range near headwaters of Kejulik River, 58.07°, -155.46° (WGS84; detailed coordinates withheld, taxon is on Alaska rare plant list), 925 m, 12 July 2017, *S. L. Ives with A. F. Wells* (ALA V177880). Rare on a partially vegetated, alpine mountain summit; soils dry, flagstones over sandy clay loam (pH 7.2). Growing with *Carex microchaeta* ssp. *nesophila* (T.Holm) A.E.Murray, *Cerastium beeringianum* Cham. & Schltdl., *Geum glaciale* Adams ex Fisch. & C.A.Mey., *Potentilla hyparctica* Malte, and *Salix rotundifolia* Trautv.

Previous knowledge. *Draba aleutica* has an Alaska state rare ranking of S2 and global rare ranking of G2 (ACCS 2019). Thus this species is considered imperiled within the state. This taxon is known to occur in Yukon and Alaska (Al-Shehbaz et al. 2010; CPNWH 2019). There are 13 previous records of this species in Alaska (ACCS 2019; ARCTOS 2019; CPNWH 2019). Ten are from the Aleutian archipelago, one from St. Paul Island, one from the east side of the Alaska Peninsula approximately 60 km south of Becharof Lake, and one from the Charley River headwaters in Yukon-Charley Rivers National Preserve.

Significance. This is the second record of this rare species on the Alaska Peninsula, and the first record in KATM. This population adds to our understanding of a species with an unusual distribution, and with substantial gaps in occurrences.

ERIOPHORUM VIRIDICARINATUM (Engelm.) Fernald (CYPERACEAE). Two collections in Lake and Peninsula Borough, KATM. First collection at Kukak Bay, 58.34°, -154.18° (WGS84; detailed coordinates withheld, taxon is on Alaska rare plant list), 32 m, 15 July 2017, *M. J. Macander with T. Christopherson, S. L. Ives, and A. F. Wells* (ALA V177885). Uncommon in a wetland on a small coastal peninsula, growing on organic soils (pH 5.9) with *Calamagrostis canadensis*, *Carex echinata* subsp. *echinata*, *Carex lyngbyei*, *Carex tenuiflora*, and *Equisetum fluviatile*. Second collection in Walatka Mountains approximately 14.5 km east of Lake Grosvenor, N 58.68°, E -154.94°, 841 m elevation, 19 August 2017, *S. L. Ives with A. F. Wells* (ALA V177886). Rare in a small wetland formed by a groundwater spring, soils of volcanic ash (pH 6.0), with *Arctagrostis latifolia* (R.Br.) Griseb., *Carex aquatilis* Wahlenb., *Carex lachenalii* Schkuhr, *Eriophorum scheuchzeri* Hoppe, and *Saxifraga rivularis* L.

Previous knowledge. *Eriophorum viridicarinatum* has an Alaska state rare ranking of S2S3 and a global rare ranking of G5 (ACCS 2019). This species is widespread in North America, occurring in 11 Canadian provinces and 20 U.S. States (Ball and Wujek 2003). In Alaska, there are 22 previous records of this species. Records are concentrated in wetlands of south-central Alaska and Kodiak Island, but also extend as far north as the southern Brooks Range, as far west as Nunivak Island, and to Chichagof and Mitkof Islands in Southeast Alaska (ACCS 2019; CPNWH 2019; ARCTOS 2019). Previous accounts of this species on National Parklands in Alaska include: Gates of the Arctic National Park and Preserve (Parker 2006), Glacier Bay National Park and Preserve (Carlson et al. 2004b), Denali National Park and Preserve (Roland 2004; Carlson et al. 2013), Wrangell-St. Elias National Park and Preserve (Cook and Roland 2002; Cook et al. 2007), and Yukon-Charley Rivers National Preserve (Roland et al. 2004).

Significance. These are the first records of this rare taxon from the Alaska Peninsula, and the first records in KATM. These populations fill a gap between the disjunct populations on Kodiak and Nunivak Islands.

LIMOSELLA AQUATICA L. (SCROPHULARIACEAE). Lake and Peninsula Borough, KATM, near the eastern shore of Kukaklek Lake, 59.18°, -155.16° (WGS84; detailed coordinates withheld, taxon is on Alaska rare plant list), 249 m, 18 August 2017, *A. F. Wells with S. L. Ives* (NPS Museum Collection KATM-00652 Cat. #55647). Rare in a barren, recently drained lake basin; soils wet, extremely gravelly loamy fine sand (pH 6.1). Growing with *Agrostis scabra* Willd., *Carex buxbaumii* Wahlenb., *Callitriche palustris* L., *Koenigia islandica* L., and *Subularia aquatica* L.

Previous knowledge. *Limosella aquatica* has an Alaska state rare ranking of S3 and global rare ranking of G5 (ACCS 2019).This taxon is known to occur in North America in Greenland, four Canadian provinces, and in nine U.S. States (ARCTOS 2019; CPNWH 2019). In Eurasia, this species is known from eastern Russia. There are 27 previous records of this species from Alaska that have location information associated with voucher specimens (ACCS 2019; ARCTOS 2019, CPNWH 2019). Records of this species in Alaska are scattered south of the Yukon River from the Alaska Range, Alaska Peninsula, Bristol Bay region, lower Kuskokwim River watershed, Kodiak Archipelago, and the north Gulf coast. Previous accounts of this species on National Parklands in Alaska include: KATM and Alagnak Wild River (Carlson and Lipkin 2003; Carlson et al. 2013), Aniakchak National Monument and Preserve (Lipkin 2005; Carlson et al. 2013), Denali National Park and Preserve (Roland 2004), Lake Clark National Park and Preserve (ACCS

2019), and Wrangell-St. Elias National Park and Preserve (Cook et al. 2007).

Significance. This is the second record of this rare species in KATM.

PRIMULA TSCHUKTSCHORUM Kjellm. (PRIMULACEAE). Lake and Peninsula Borough, KATM, approximately 4 km northwest of the outlet of Mirror Lake, 59.27°, -154.82° (WGS84; detailed coordinates withheld, taxon is on Alaska rare plant list), 501 m, 26 August 2017, *G.V.Frost with S. L. Ives and R.W. McNown* (NPS Museum Collection KATM-00652 Cat. #55601). Rare in an alpine wet sedge meadow; soils wet, organic over very cobbly till (pH 6.1), growing with *Carex aquatilis*, and *Carex rotundata* Wahlenb., *Eriophorum angustifolium* Honck., *Sarmenthypnum sarmentosum* (Wahlenb.) Tuom. & T. Kop., and *Sphagnum lindbergii* Schimp.

Previous knowledge. *Primula tschuktschorum* has an Alaska state rare ranking of S3 and global rare ranking of G2G3 (ACCS 2019). A state ranking of S3 means this species is rare within the state and at moderate risk of extirpation. A global ranking of G2G3 is suggestive of a moderate level of vulnerability at the global level. As the subnational rank was increased to a rank greater than the global rank, the global rank will increase to the minimum subnational rank (G3 in this case). This taxon is known to occur in North America only in Alaska (Kelso 2009; CPNWH 2019). Outside of North America, this species is known from eastern Russia in the Being Strait region (ARCTOS 2019). There are 82 previous records of this species in Alaska all from the Bering and southern Chukchi Sea regions, and northern Alaska Peninsula (ACCS 2019; ARCTOS 2019; CPNWH 2019). Records of this taxon are concentrated on the Seward Peninsula, the Ahklun and Wood River Mountains, the northern Alaska Peninsula, Cape Lisburne, and several islands in the Bering Sea: Nunivak, St. George, St. Matthew, and St. Lawrence. Previous accounts of this species on National Parklands in Alaska include: Bering Land Bridge National Preserve (Parker 2006) and KATM (Carlson and Lipkin 2003; Carlson et al. 2013). The taxonomy and identification of this taxon has been inconsistent; furthermore *P. tschuktschorum* is known to hybridize with *P. eximia* Greene (Carlson et al. 2008), making descriptions of its distribution problematic.

Significance. This is the third record of this rare species in KATM and at the southern edge of its range.

GNAPHALIUM ULIGINOSUM L. (ASTERACEAE). Lake and Peninsula Borough, KATM, approximately 1.6 km south of the southern shore of Kukaklek Lake, 59.11287°, -155.28563° (WGS84), 341 m, 15 August 2017, *S. L. Ives with A. F. Wells* (ALA V177887). Uncommon in a partially vegetated, recently drained lake basin on moist, very gravelly sandy loam soils (pH 6.1), with *Agrostis scabra*, *Carex kelloggii* W.Boott, *Carex saxatilis* L., and *Deschampsia cespitosa* (L.) P.Beauv.

Previous knowledge. *Gnaphalium uliginosum* is native to Europe, and is presently known to occur in North America in 12 Canadian provinces, and in 29 U.S. states (Nesom 2006). This species is generally considered non-native to North America; however, it is unclear if some or all of the North American plants were introduced (Nesom 2006). *Gnaphalium uliginosum* is considered non-native in Alaska (AKEPIC 2019).The earliest known records in Alaska are from Fairbanks in 1931 and the village of Takotna in 1941 (CPNWH 2019). There are 19 previous records, ranging from as far south as Prince of Wales Island in Southeast Alaska to as far north as Minto Flats, and as far west as the Togiak River, approximately 26 km upstream of the village of Togiak. In KATM, a likely vector for propagules is fly-in fishing operations, which are common in this part of the park during summer.

Significance. This represents the first record on the west side of the Aleutian Range on the Alaska Peninsula, is the first record in KATM, and is one of the few non-native plants established in areas away from human development in the state.

PHLEUM PRATENSE L. (POACEAE). Lake and Peninsula Borough, on an exposed headland at Cape Atushagvik , 58.08333°, -154.31872° (WGS84), 3 m, 17 July 2017, *M. J. Macander with T. Christopherson* (NPS Museum Collection KATM-00652 Cat. # 55404). Uncommon in a moist meadow; soils organic over gravelly coarse sand (pH 4.7), with *Angelica genuflexa* Nutt., *Empetrum nigrum* L., *Carex macrochaeta* C.A.Mey., *Chamaepericlymenum suecicum* (L.) Asch. & Graebn., and *Viola langsdorffii* Fisch. ex Ging.

Previous knowledge. *Phleum pratense* is native to Europe and is considered non-native in North America, where it is presently known to occur in all Canadian provinces except Prince Edward Island and Labrador, and in all 50 U.S. States (Esser 1993). Carlson and Shephard (2007) developed an invasiveness ranking system for Alaska, which ranks non-native species on a scale from 0 (no threat to native ecosystems) to 100 (major threat). *Phleum pratense* has been assigned an invasiveness ranking of 54, indicating it represents a moderate threat to native ecosystems. Previously known records in Alaska occur from as far south as Prince of Wales Island in Southeast Alaska, to as far north as Fairbanks, and as far west as Nome (AKEPIC 2019; ARCTOS 2019; CPNWH 2019). This species is also known from Unalaska Island in the Aleutian archipelago. NPS IRMA (2019) reports that this non-native species occurs in the following National Parks in Alaska: Glacier Bay National Park and Preserve, KATM, Kenai Fjords National Park, Klondike Gold Rush National Historical Park, Kobuk Valley National Park, Lake Clark National Park and Preserve, Sitka National Historical Park, Wrangell-St. Elias National Park and Preserve, and Yukon-Charley Rivers National Preserve.

The presence of this non-native species in such a remote location is somewhat puzzling. One possible vector is seeds attached to the fur of bears traveling to and from Hallo Bay and Geographic Harbor, popular bear viewing areas along the KATM coast. This grass has a long history as a pasture grass in Alaska, including at a few remote locations, hence the source could be from an abandoned homestead (M. L. Carlson, University of Alaska, Anchorage, personal communication). For example, *P. pratense* was encountered in 2005 on the far eastern end of Tustumena Lake at an old cabin site near Glacier Creek (AKEPIC 2019). However, while a large pre-contact village occupied Cape Atushagvik until ca. AD 1300, no homesteads are known from the area (K. Meyers, U.S. National Park Service, Anchorage, AK, personal communication). In the early 1900s explorers and scientists in the Katmai region, many of whom used horses, may have transported *P. pratense* to the area on their way to the Valley of 10,000 Smokes. However, most began their journey from Katmai Bay, or further south at the village of Kanatak (Hildreth and Fierstein 2012), and it seems unlikely any would have passed by Cape Atushagvik, an approximate 80 km trek across a rugged coastline from Katmai Bay. Horses are another possible vector for propagules of *P. pratense*. In 1956, a barge carrying 16 horses from Kodiak to Puale Bay in rough seas began taking on water (Clemens and Norris 1999). The skipper pulled into nearby Amalik Bay, unloaded the horses, and went back to Kodiak. The horses eventually scattered, and all but one of them died within six months. The surviving horse, a bay gelding, was spotted each year by fishermen and pilots for the next 18 years until a fisherman found its carcass in 1974, surrounded by wolf tracks.

Significance. This represents the first confirmed specimen record of this species in KATM, and the only specimen on the Shelikof Strait side of the Alaska Peninsula. A number of records are known from the Bristol Bay side of the peninsula at the settlement of King Salmon, less than 10 km west of the KATM Park boundary (AKEPIC 2019).

PERSICARIA LAPATHIFOLIA (L.) Gray (POLYGONACEAE). Lake and Peninsula Borough, KATM, on a sand bar of an unnamed river that flows into the south end of Brooks Lake, 58.43182°, -156.17244° (WGS84), 34 m, 18 August 2016, *E. K. Johnson with T. Christopherson* (NPS Museum Collection KATM-00652 Cat. #54535). Rare in a willow thicket; soils very fine sandy loam over extremely gravelly coarse sand (pH 6.1), with *Calamagrostis canadensis*, *Equisetum arvense* L., and *Polygonum aviculare* L., *Salix alaxensis*, and *Salix barclayi* Andersson.

Previous knowledge. *Persicaria lapathifolium* is native to North America, but is considered non-native in Alaska (Hultén 1968, Welsh 1974), and has been assigned an invasiveness ranking of 47, indicating it represents a moderate threat to native ecosystems (AKEPIC 2019). This taxon is presently known to occur in North America in Greenland, in 13 Canadian provinces, and in all 50 U.S. states (Hinds and Freeman 2005). Globally, this taxon is known to occur in Mexico, South America, Europe, Asia, Africa, and New Zealand. Previously known records in Alaska extend from as far south as Juneau in Southeast Alaska, to as far north as the Kobuk River in Kobuk Valley National Park, and as far west as the Innoko River (ARCTOS 2019; CPNWH 2019). This species is also known from Kodiak Island in the Gulf of Alaska. NPS IRMA (2019) reports, and specimen records confirm, that this species occurs in the following National Parks in Alaska: Denali National Park and Preserve, KATM, Kobuk Valley National Park, Lake Clark National Park and Preserve, and Yukon-Charley Rivers National Preserve.

Significance. This represents the second record of this non-native species in KATM, and it is the most southerly record on the Alaska Peninsula.

—AARON F. WELLS, SUSAN L. IVES, ERIN K. JOHNSON[†], ABR, Inc., Environmental Research & Services, P.O. Box 240268, Anchorage, AK 99524. awells@abrinc.com; MATTHEW J. MACANDER AND GERALD V. FROST, ABR, Inc., Environmental Research & Services, P.O. Box 80410, Fairbanks, AK 99708.
[†] Deceased

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THE CALIFORNIA PHENOLOGY COLLECTIONS NETWORK: USING DIGITAL IMAGES TO INVESTIGATE PHENOLOGICAL CHANGE IN A BIODIVERSITY HOTSPOT

Jenn M. Yost[1] and Katelin D. Pearson
Robert F. Hoover Herbarium, Biological Sciences Department,
California Polytechnic State University, San Luis Obispo, CA 93407-0401
[1]jyost@calpoly.edu

Jason Alexander
University and Jepson Herbaria, University of California, Berkeley, CA 94720

Edward Gilbert
School of Life Sciences, Arizona State University, Tempe, AZ 85287

Layla Aerne Hains
SD Herbarium, San Diego Natural History Museum, San Diego, CA 92101

Teri Barry
UC Davis Center for Plant Diversity, Plant Sciences M.S. 7,
One Shields Ave., Davis, CA 95616

Robin Bencie
Vascular Plant Herbarium, Humboldt State University, Arcata, CA 95521

Peter Bowler
UCI Arboretum and Herbarium, University of California, Irvine, CA 92697

Benjamin Carter
Carl W. Sharsmith Herbarium and Department of Biological Sciences,
San Jose State University, San Jose, CA 95192

Rebecca E. Crowe
UCI Arboretum and Herbarium, University of California, Irvine, CA 92697

Ellen Dean
UC Davis Center for Plant Diversity, Plant Sciences M.S. 7,
One Shields Ave., Davis, CA 95616

Joshua Der
Department of Biological Science, California State University, Fullerton, CA 92834

Amanda Fisher
Department of Biological Sciences, Long Beach State University, Long Beach, CA 90840

Kirsten Fisher
CSLA Herbarium, California State University, Los Angeles, Los Angeles, CA 90032

Lluvia Flores-Renteria
Department of Biology, San Diego State University, San Diego, CA 92182

C. Matt Guilliams
Clifton Smith Herbarium, Santa Barbara Botanic Garden, Santa Barbara, CA 93105

Colleen Hatfield
Chico State Herbarium, Department of Biological Sciences,
California State University, Chico, CA 95929

Larry Hendrickson
Colorado Desert District, California Department of Parks and Recreation,
Borrego Springs, CA 92004

TOM HUGGINS
UCLA Herbarium, University of California, Los Angeles, CA 90095

LAWRENCE JANEWAY
Chico State Herbarium, Department of Biological Sciences,
California State University, Chico, CA 95929

CHRISTOPHER LAY
Norris Center for Natural History, University of California, Santa Cruz, CA 95064

AMY LITT
Department of Botany & Plant Sciences, University of California, Riverside, CA 92521

STACI MARKOS
University and Jepson Herbaria, University of California, Berkeley, CA 94720

SUSAN J. MAZER
Department of Ecology, Evolution and Marine Biology,
University of California, Santa Barbara, CA 93106

DANNY MCCAMISH
Colorado Desert District, California Department of Parks and Recreation,
Borrego Springs, CA 92004

LUCINDA MCDADE
Rancho Santa Ana Botanic Garden, Claremont, CA 91711

MICHAEL MESLER
Vascular Plant Herbarium, Humboldt State University, Arcata, CA 95521

BRENT MISHLER
University and Jepson Herbaria, University of California, Berkeley, CA 94720

MARE NAZAIRE
Rancho Santa Ana Botanic Garden, Claremont, CA 91711

JON REBMAN
SD Herbarium, San Diego Natural History Museum, San Diego, CA 92101

LARS ROSENGREEN
Carl W. Sharsmith Herbarium and Department of Biological Sciences,
San Jose State University, San Jose, CA 95192

PHILIP W. RUNDEL
Department of Ecology and Evolutionary Biology,
University of California, Los Angeles, CA 90095

DAN POTTER
Department of Plant Sciences, University of California, Davis, CA 95616

ANDREW SANDERS
Herbarium, Department of Botany & Plant Sciences,
University of California Riverside, CA 92521

KATJA C. SELTMANN
Cheadle Center for Biodiversity and Ecological Restoration,
University of California, Santa Barbara, CA 93106

MICHAEL G. SIMPSON
Department of Biology, San Diego State University, San Diego, CA 92182

GREGORY A. WAHLERT
Cheadle Center for Biodiversity and Ecological Restoration,
University of California, Santa Barbara, CA 93106

KATHERINE WASELKOV
Department of Biology, California State University, Fresno, CA 93740
KIMBERLYN WILLIAMS
Biology Department, California State University San Bernardino, San Bernardino, CA 92407
PAUL S. WILSON
Department of Biology, California State University, Northridge, CA 91330

ABSTRACT

The California Phenology Thematic Collections Network (CAP TCN) is a collaborative project that seeks to maximize the value of herbarium specimens and their data, especially for understanding changes in plant phenology due to anthropogenic climate change. The project unites personnel in herbaria at California universities, research stations, natural history museums, and botanic gardens with the goal of capturing images, transcribing label data, and producing georeferenced coordinates of nearly one million preserved plant specimens collected over the past 150+ years. Each digitized specimen will also be scored for its phenological status—the stage of growth and reproduction of the specimen such as flowering or fruiting. The CAP TCN is developing efficient workflows and data standards necessary to collect, store, and analyze trait data from specimens to ensure their utility for research and other applications. These novel resources and data will enable powerful research in phenology and other topics in the California Floristic Province biodiversity hotspot and beyond.

Key Words: ADBC – NSF, California Consortium of Herbaria (CCH), digitization, herbarium, iDigBio, natural history collections, phenology, specimens, thematic collections network.

Dried, pressed plant specimens preserved in herbaria have been essential sources of biodiversity data for centuries (Lavoie 2013). In the modern information era, data from specimens are being used for an increasing number of purposes, for example, documenting plant distributions in time and space and allowing for comparisons of plant morphology, biochemistry, and genetic variation among individuals, taxonomic groups, and lineages (Pyke and Ehrlich 2010; Lavoie 2013; Thornhill et al. 2017; Meineke et al. 2018a; Lang et al. 2018). Herbarium specimens have also proven critical in areas of major societal concern, such as understanding the effects of anthropogenic change due to pollution (Peñuelas and Filella 2002; Zschau et al. 2003), land-use change (Case et al. 2007), and climate change (Calinger et al. 2013; Wolf et al. 2016; González-Orozco et al. 2016), among other topics. For example, spatiotemporal specimen data have enabled researchers to track the spread of economically important invasive species (Chauvel et al. 2006), identify changes in the distributions of native species (Farnsworth and Ogurcak 2006; Case et al. 2007), and establish conservation priorities for vulnerable taxa (Kling et al. 2018).

Herbarium digitization—capturing standardized label data and high-resolution images of herbarium specimens—makes large amounts of high-quality data readily and globally available online, which accelerates research and facilitates the development of new research tools and methods (Elith et al. 2006; James et al. 2018; Pearson 2018). Specimen images, in particular, have opened doors to new avenues of research, including automated species identification of herbarium specimens (Carranza-Rojas et al. 2017) and the detection of shifts in plant phenological events in response to climate change (Willis et al. 2017). Digital specimen images may also accelerate characterization of other plant features such as evidence of herbivory (see Meineke et al. 2018b) or disease (see Antonovics et al. 2003).

Despite its importance for advancing research, herbarium specimen digitization remains an enormous task for the world's herbaria. In California, herbarium digitization has been underway since the early 1990s and was accelerated with the establishment of the Consortium of California Herbaria in 2003 (CCH; http://ucjeps.berkeley.edu/consortium/about.html), which has since grown to include 2.2 million specimen records from 40 institutions. Even with these efforts, digitization is far from complete in the state's herbaria; hundreds of thousands of specimens remain in analog format only, and only 7% of currently digitized California specimens have been imaged as of March 2019, according to the national data aggregator iDigBio (idigbio.org). While label data alone can be used to address certain scientific questions, high-resolution images of herbarium specimens are necessary for verifying taxon identification and to provide data regarding plant traits that can be scored upon visual inspection, including plant size, vegetative or floral herbivory, evidence of pathogens, morphology, and precise reproductive status.

The California Phenology Thematic Collections Network (CAP TCN; https://www.capturingcaliforniasflowers.org/) was established by a grant from the Advancing Digitization of Biodiversity Collections (ADBC) program of the United States National Science Foundation. The CAP TCN aims to generate nearly one million high-resolution images of herbarium specimens from 22 California institutions. Each specimen record will consist of an image, transcribed label data, georeferenced coordinates when possible, and phenological data. To share these data widely, the CAP TCN has established a new web-accessible database system (cch2.org) available for use by researchers, land managers, educators, and any member of the public. Along with specimen collection dates, the reproductive status (e.g., the presence or number of unopened or open flowers, inflorescences, or mature or dehiscing fruits) of all imaged specimens will be scored and comprise the basis of a significant phenological dataset that can be used to study the effects of climate change on the seasonal cycles of plants in California, a biodiversity hotspot.

California has the most diverse native flora of any state in the U.S., containing more than one third of all U.S. plant species. The state is considered a biodiversity hotspot due to its high diversity, high number of endemic taxa, and major threats (Raven and Axelrod 1978; Myers et al. 2000; Baldwin et al. 2012, 2017). The state's flora includes nearly 7,700 minimum-rank taxa (including species and infraspecific taxa), of which 6,572 (85%) are native and 2,303 (30%) are endemic (Jepson Flora Project 2019). This diverse and highly endemic flora is also highly endangered; the California Native Plant Society classifies about one third of the state's native taxa as taxa of special conservation concern (CNPS 2018), and nearly 4% of taxa are state or federally listed as endangered, threatened, or rare (CDFW 2019). In this context, rapid land use changes and anthropogenic climate change pose a heightened threat to the California flora. The rising temperatures predicted by climate models are already being observed in California (Parmesan and Yohe 2003; Kelly and Goulden 2008), and this change is impacting the state's plants (Rapacciuolo et al. 2014). Understanding how plant species, populations, and communities change with time and space across the state is critical to directing conservation efforts, land management, and future scientific inquiry. By producing thorough, high quality data records, georeferenced coordinates, and images of nearly one million herbarium specimens, the CAP TCN digitization project will greatly advance our understanding of the state's flora.

Phenology

Investigating changes in plant phenology, the timing of plant growth and reproduction, is a key application for the data produced by the CAP TCN. Phenological change is one of the most significant and widely recognized effects of climate change (Walther et al. 2002; Parmesan and Yohe 2003; Calinger et al. 2013; Willis et al. 2017), and such change may pose a heightened threat to the California flora (Loarie et al. 2008). Numerous ecological functions depend on plant phenology at multiple levels of biological organization, from individuals to ecosystems. Phenology not only affects the individual fitness of plants, but also the fitness of organisms that depend on plants, such as mutualistic pollinators and seed-dispersers or antagonistic herbivores and parasites (Visser and Both 2005; Both et al. 2006). This in turn can affect population-level processes such as population growth, mating patterns, gene flow, and evolution (Franks and Weis 2009; Ozgul et al. 2010; Anderson et al. 2012). For example, temporal mismatches between plants and pollinators can extirpate local populations of both members of a mutualistic pair, cause rapid evolutionary shifts, and result in billions of dollars of agricultural losses (Memmott et al. 2007; McKinney et al. 2012; Kudo and Ida 2013; Miller-Struttmann et al. 2015). As climate change progresses, phenology-dependent interactions between plants and their mutualists and antagonists will likely change with unknown consequences for biodiversity or agricultural systems (Encinas-Viso et al. 2012; Matthews and Mazer 2016). Understanding changes in plant phenology is important not only to improve our understanding of—and our ability to forecast—ecological change but also to address practical environmental problems in both agricultural and natural settings.

Herbarium specimens preserve invaluable phenological data for thousands of plants across time and space. Although most herbarium specimens are not generally collected with the purpose of conducting phenological research, the phenological status of a specimen can usually be ascertained from reproductive structures visible on the sheet. The use of herbarium specimens to track the relationship between local climatic conditions and the collection dates of flowering specimens has a relatively short history (Willis et al. 2017). Nevertheless, several herbarium-based studies have corroborated the link between phenological events and climate change that was first observed in long-term, place-based studies (Primack et al. 2004; Lavoie and Lachance 2006; Davis et al. 2015; Willis et al. 2017), despite known geographic, temporal, and taxonomic biases of herbarium records (Daru et al. 2017). These studies have improved our understanding of narrow- and broad-scale phenological shifts among many taxa and in many regions across the globe (Willis et al. 2017). They have also elucidated the specific advantages of herbarium specimens for phenological research, such as filling gaps in long-term or observational data sets for a period of time (Meyer et al. 2016; Willis et al. 2017), underrepresented regions (Li et al. 2013), and threatened or rare taxa (Robbirt et al. 2011).

Digitizing California's herbaria will unlock long-term phenological records for nearly a million specimens, some of which date back to the late 1800s. With these data, researchers will be able to generate an unprecedented picture of the relationship between phenology and climate change in California and how this relationship varies with different taxa and phenophases (phases within a phenological event, such as full flowering or end of flowering). The phenological data generated by this project will help answer questions such as: (1) To what extent can

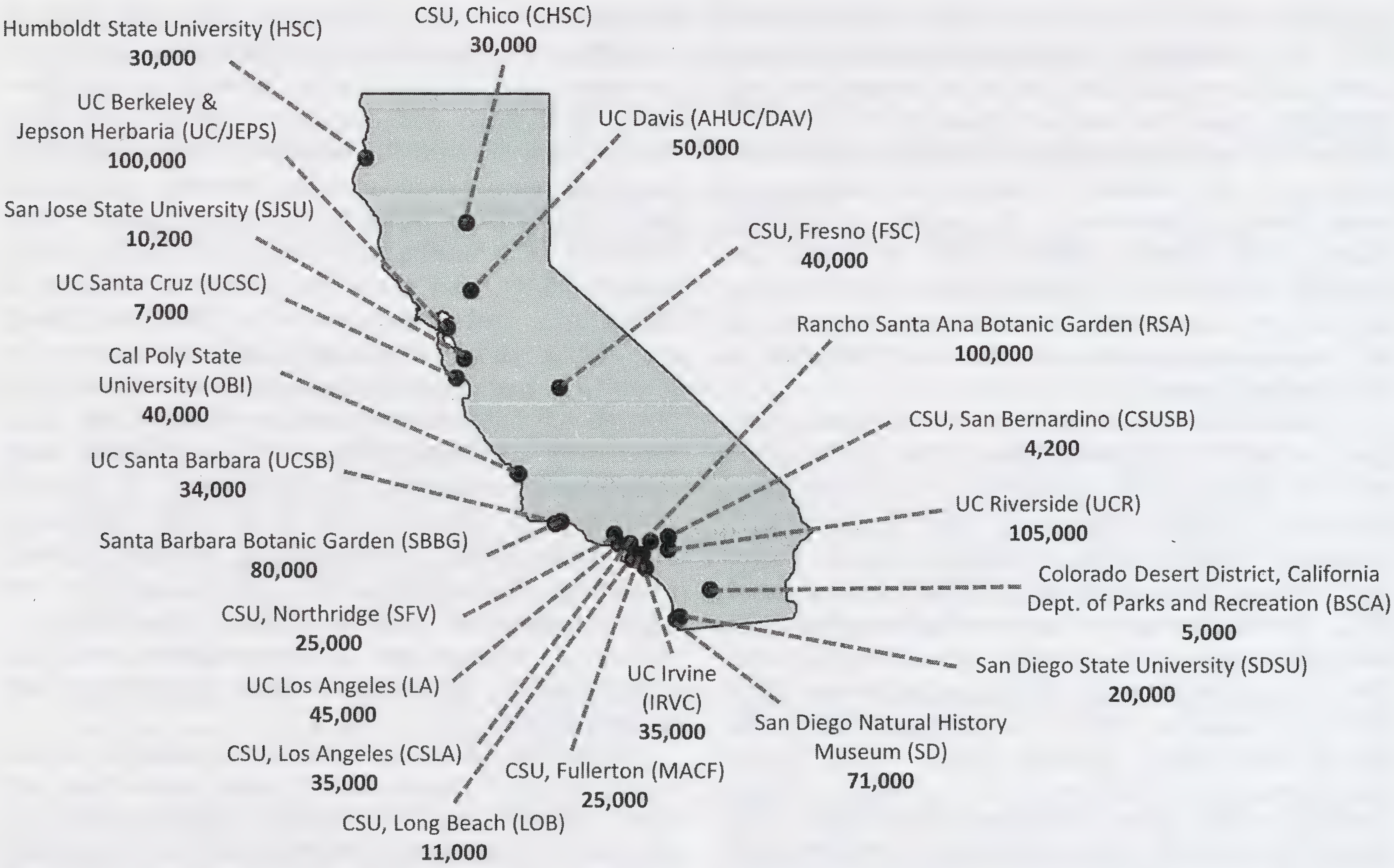

FIG. 1. Map of collaborating institutions in the CAP TCN as of 2018. Herbarium acronyms as documented in Index Herbariorum (Thiers 2019) are provided in parentheses. The acronyms CSU and UC denote California State University and University of California, respectively. The target number of images to be produced by each institution is listed under the institution name.

observed phenological sensitivities to climate conditions be generalized among, for example, congeneric species, confamilial genera, or distinct families? (2) Are the flowering times of individual taxa more strongly associated with climate normal values (mean climate values over 30 years), suggesting that flowering time has evolved in response to long-term climatic conditions, or with climate conditions in the single year or season preceding the collection date? (3) For which species, genera, families, vegetation types, or functional groups do multivariate phenoclimate models best predict flowering times? (4) Which habitats and vegetation types are most phenologically sensitive to changes in precipitation and temperature? (5) Do different functional groups (e.g., evergreen versus deciduous taxa, annual herbs, geophytes) differ in their responses to long-term changes in temperature and precipitation? (6) Are rare species more (or less) phenologically sensitive to climate than widespread species? (7) Do the phenological sensitivities of species occupying highly water-limited habitats (e.g., deserts, serpentine outcrops, south-facing slopes) differ from those of species occupying more mesic habitats? and (8) In systems for which we have phenological data on pollinators, pathogens, and pests, where might phenological mismatches occur between flowering plant species, including agricultural plants, and these interacting taxa? In addition, with more robust assessments of the phenological status of herbarium specimens, along with historical and contemporary climatic data available online through PRISM (Daly et al. 1994, 2008) and ClimateNA (Wang et al. 2016), researchers will be poised to generate novel predictions concerning the effects of upcoming climate change on the seasonal cycles of individual California plant species and the communities that they constitute (cf. Park et al. 2019; Park and Mazer 2018, 2019).

Phenological research—though important in itself—is only the beginning of the many applications for digital specimen images, and the potential for these specimens and their associated data to enhance our understanding of ecology, systematics, evolution, biodiversity, and the effects of anthropogenic change is rapidly increasing. The CAP TCN empowers this research, unites and supports existing data-providers, and makes new resources available for the exploration of natural history collections.

PARTICIPANTS

The CAP TCN currently comprises 22 California institutions: 11 California State University campuses, seven University of California campuses, two botanic gardens, one natural history museum, and one California Department of Parks and Recreation research station (Fig. 1). Over the duration of this project, hundreds of undergraduates and members of

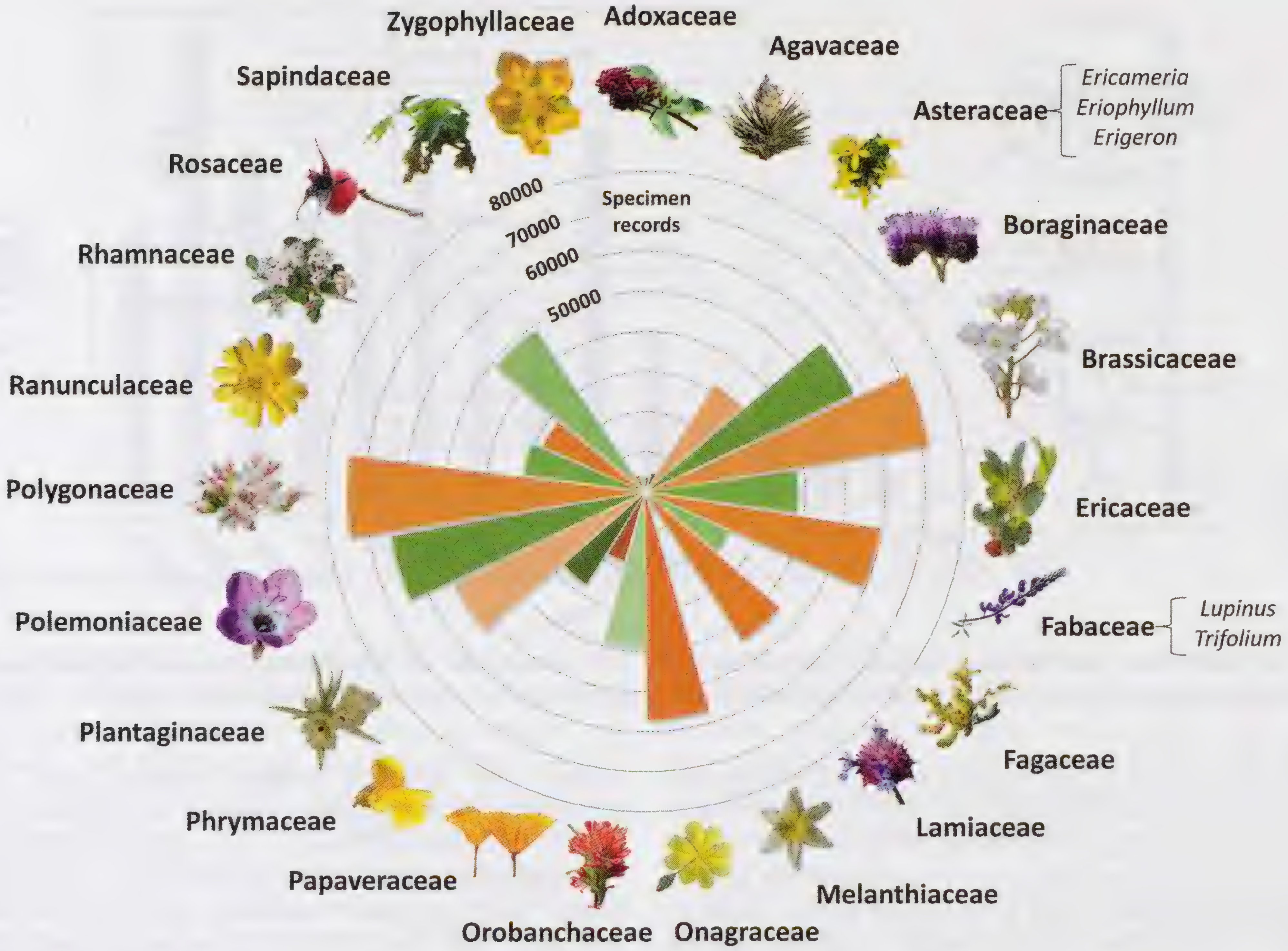

FIG. 2. Target families to be digitized for the CAP TCN project. Each radial bar indicates the number of specimen records of that family that will have phenological data and images in the CAP data portal, CCH2.

the public will engage with California's herbaria and learn about the importance of natural history collections. The project is directed by California Polytechnic University, San Luis Obispo (OBI) with additional leadership from UC Berkeley (UC/JEPS) and UC Santa Barbara (UCSB). Despite ambitious digitizing efforts among California herbaria in the past, prior to the CAP TCN, only a few herbaria had generated images of their specimens (RSA, SD, SDSU, SJSU, UC/JEPS, and UCSB). In the future, hopefully every specimen in California herbaria will be accompanied by a high-resolution image available online.

PROJECT GOALS

The sheer number of plant specimens in California herbaria precludes imaging all of them in a single project. Therefore, to build the most robust dataset for detecting phenological shifts, the CAP TCN is targeting the oldest records, the most diverse families, and the families with the most endemic and threatened taxa (Fig. 2). These families also include many species that represent model systems for evolutionary research; the families Asteraceae, Brassicaceae, Onagraceae, Phyrmaceae, and Polemoniaceae have been the focus of years of research in systematics and evolutionary biology. In addition, the CAP TCN is targeting the Adoxaceae, Agavaceae, Sapindaceae, Zygophyllaceae, and an additional 250 taxa that are currently monitored by the USA National Phenology Network (usanpn.org) and the California Phenology Project (cpp.usanpn.org) to provide robust comparisons between the historical record of plant phenology (based on herbarium specimens; Fig. 3) and the contemporary record (based on *in situ* observations of living plants; Haggerty et al. 2013; Matthews et al. 2014). In total, the CAP TCN aims to make available 904,200 imaged, fully databased, and georeferenced herbarium specimen records. The project will also produce phenological scores (e.g., annotations of unopened flowers, open flowers, and fruit) of all 904,200 specimens according to cooperatively-developed phenological standards and protocols.

PROJECT IMPLEMENTATION

Equipment and Workflows

Producing such a large number of specimen images within four years requires new equipment, efficient protocols, training, and, most importantly, strong collaboration. Fortunately, the CAP TCN operates within the collaborative network of other ADBC-funded digitization projects, such as the Mid-Atlantic Megalopolis TCN and Southeastern Collaborative Network of Expertise and Collections

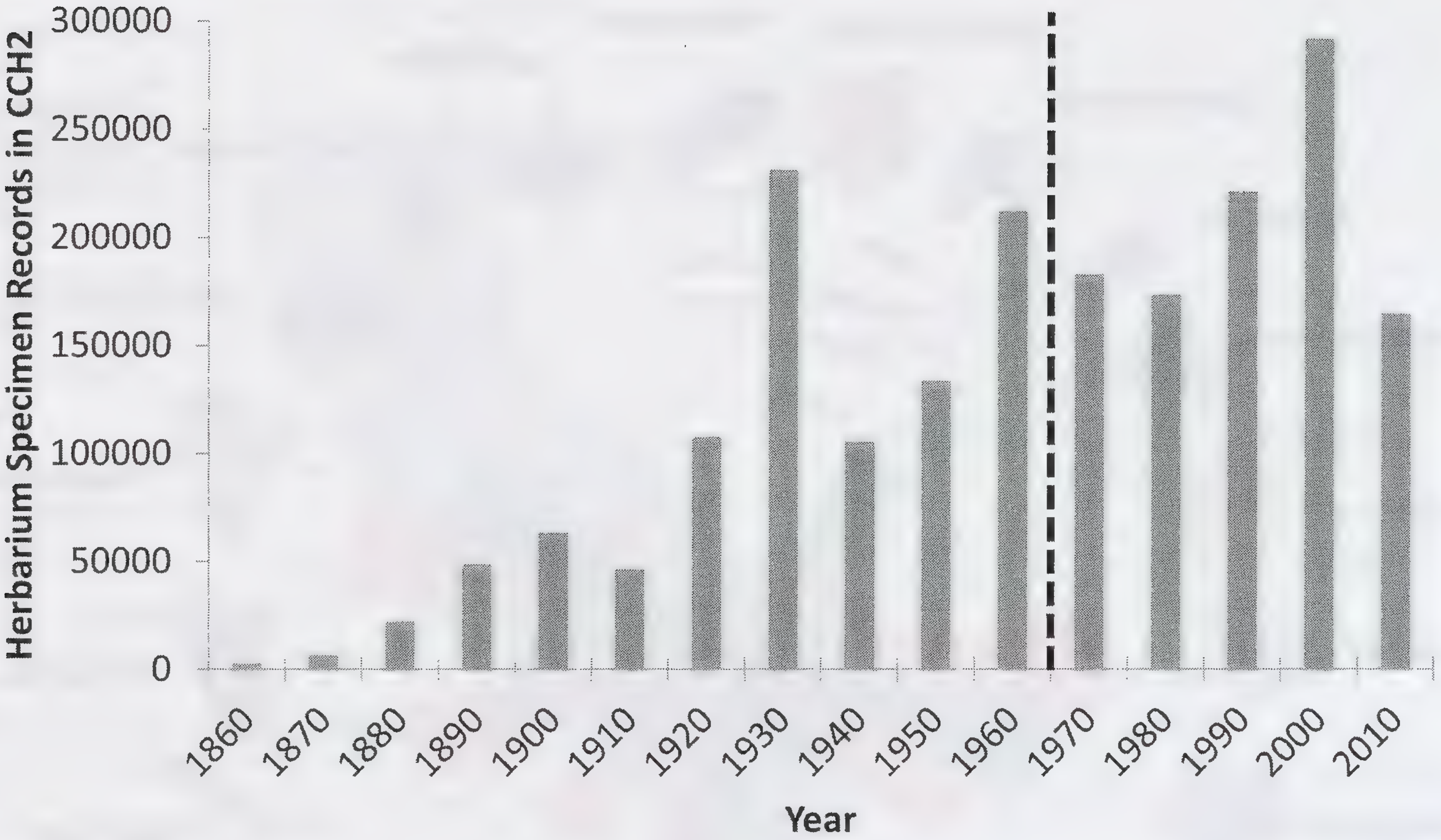

FIG. 3. Numbers of herbarium specimen records in the CAP TCN data portal, CCH2, according to date of collection. The approximate onset of recent climate warming is indicated by the black dashed line (Hodgkins et al. 2003).

(SERNEC), both of which have provided instrumental guidance in establishing CAP TCN protocols and best practices. Representatives of most CAP TCN participating institutions (Fig. 1) attended the ADBC Summit in October 2018 to kickstart active communication and receive initial training. Institutions have purchased and assembled new imaging stations, each including a high-resolution camera, lighting equipment, and necessary software for capturing and processing images. CAP leadership is constantly developing workflows and protocols for use across the network, drawing heavily from existing resources and best practices disseminated by iDigBio (idigbio.org), other Thematic Collections Networks, and other herbaria. While each herbarium in the CAP TCN adapts these workflows and protocols to fit their own institution, they all begin with an understanding of digitization best practices, and, as a result, the images and data meet a specified standard of quality. Site-visits, webinars, and conference calls with the project manager build capacity at each herbarium and ensure that project goals are met. The developed resources, including training manuals, videos, protocols, and quarterly reports, are publicly available on the project website: capturingcaliforniasflowers.org. A simplified diagram of the CAP TCN digitization workflow is shown in Figure 4.

Data Portal

Once specimen images are produced and processed, they are made available online through a new specimen data portal, CCH2 (cch2.org). The CCH2 portal contains all specimen data—regardless of taxon or collection location—from all collaborating institutions. This portal greatly expands institutions' abilities to curate and digitize specimens because it leverages Symbiota, an open source content management system that enables storage, sharing, and active curation of specimen data (symbiota.org; Gries et al. 2014). Symbiota software, and thus the CCH2 portal, contains numerous data curation and management tools, such as data cleaning and georeferencing modules. The CAP TCN is developing new tools to capture phenological data from specimen images (see Phenological Scoring), and several of these tools can be co-opted to capture other trait data (e.g., leaf measurements, herbivore damage).

Previously, many herbaria in the CAP TCN lacked interoperable databases that allowed efficient curation, cleaning, and sharing of specimen data. Now, using a web browser, each herbarium can actively manage its own data in the CCH2 portal, and data managers, users, and the public can view images and data, including phenological data, from these collections as soon as information is added. Institutions with managers who prefer to manage specimen data in a local database can still share their data by regularly uploading a "snapshot" of their dataset to the portal, which also becomes publicly accessible upon upload. Data entered in the CCH2 portal, either "live" or through a "snapshot" upload, are automatically mapped to biodiversity data standards provided by Darwin Core (Wieczorek et al. 2012b), promoting interoperability of data between institutions worldwide. Also because of these standards, CCH2 data are easily parsed and distributed via global data aggregators iDigBio (idigbio.org) and GBIF (gbif.org). The earlier California Consortium of Herbaria public interface, now known as CCH1 (http://ucjeps.berkeley.edu/consortium/), will also draw from the CCH2 portal and display only data from vascular plant specimens collected in California, integrating closely with the Jepson eFlora (http://ucjeps.berkeley.edu/eflora/).

The new CCH2 portal will be used to georeference all targeted specimens that have not already been

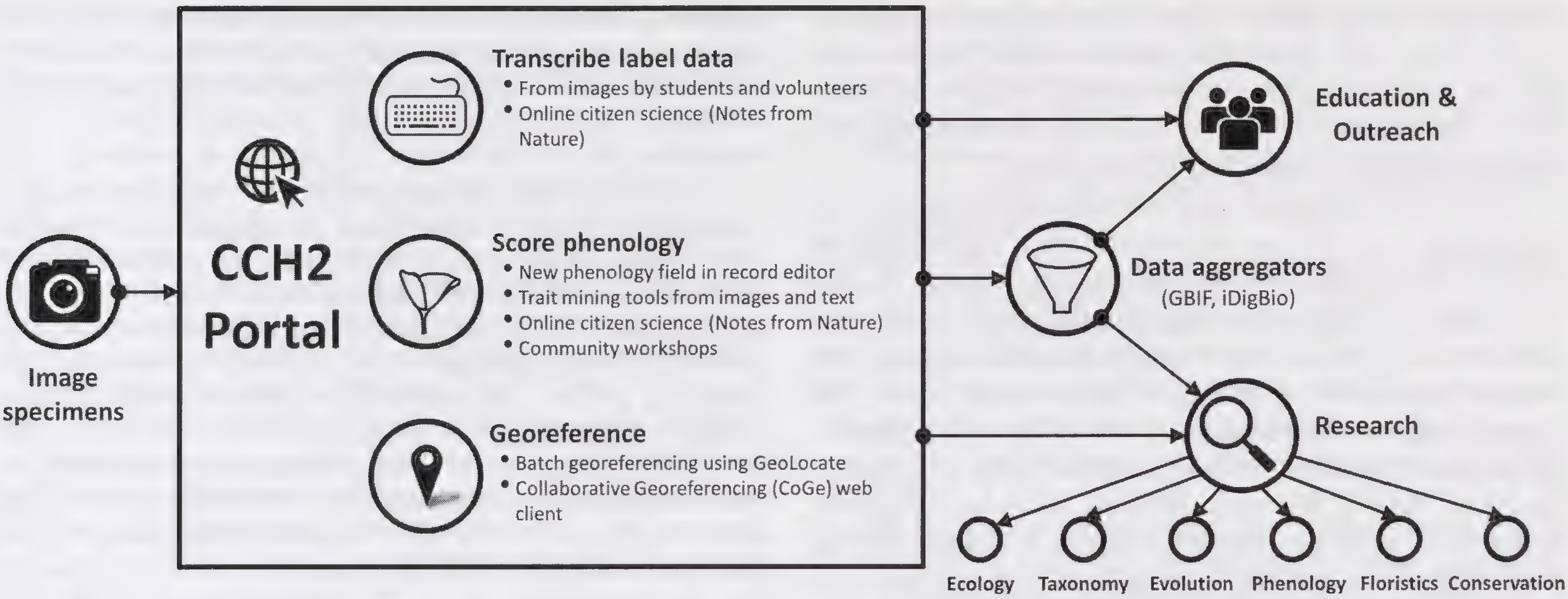
Image specimens
CCH2 Portal
Transcribe label data
From images by students and volunteers
Online citizen science (Notes from Nature)
Score phenology
New phenology field in record editor
Trait mining tools from images and text
Online citizen science (Notes from Nature)
Community workshops
Georeference
Batch georeferencing using GeoLocate
Collaborative Georeferencing (CoGe) web client
Education & Outreach
Data aggregators
(GBIF, iDigBio)
Research
Ecology
Taxonomy
Evolution
Phenology
Floristics
Conservation

FIG. 4. Simplified diagram of the CAP TCN workflow from image capture to data use.

assigned latitude and longitude coordinates in previous projects (e.g., Baldwin et al. 2017). The CCH2 portal, like most Symbiota instances, is equipped with GEOLocate (Rios and Bart 2010), batch georeferencing tools, and botanical duplicate identification tools, each of which will facilitate efficient georeferencing of herbarium specimen records according to existing community-established protocols (Fig. 4; Wieczorek et al. 2012a).

Phenological Scoring

To capture phenological data, the CAP TCN is developing workflows for scoring phenology in a number of ways (Fig. 4). Once phenological data standards are established and appropriate tools are developed in the data portal, some institutions may capture phenological traits concurrently with other digitization steps (e.g., label transcription). The new phenological data fields on the occurrence record page of the portal, developed for this project, will greatly facilitate this process. The project is also expanding the Image Scoring Tool, a Symbiota module developed for the New England Vascular Plants Thematic Collections Network (nevp.org). The Image Scoring Tool presents users with images of specimens and allows them to apply a score (e.g., "unopen flowers absent, open flowers present, and fruit present") to each record. These scores are recorded as annotations to the specimen record according to Darwin Core-compatible standards (see Yost et al. 2018 for proposed scoring schema), which will be fully interoperable with phenological data produced by other means via mapping to the Plant Phenology Ontology (Stucky et al. 2018).

The project will also use and build upon another newly-developed Symbiota function, the Attribute Mining Tool. This tool allows editors to search any database field for certain words that refer to reproductive states and apply a phenological score according to set definitions. For example, an editor can search the "Notes" field of the database for the word "flower" and all unique text strings containing "flower" will be shown. The editor can then select all records that are suitable and apply the same phenological score to all selected records at once. This tool greatly facilitates adding trait attributes to records and could be expanded for any number of other traits.

Some phenological scores will be produced via crowdsourcing using the citizen science platform Notes from Nature (notesfromnature.org; see below). These scores will represent the consensus scores offered by at least three independent volunteer scorers, requiring expert review only when results are ambiguous. Finally, there are many opportunities to explore automated phenological scoring of herbarium specimen images. Investigators at several collaborating institutions, as well as the CAP TCN project manager, are exploring the use of machine learning (e.g., neural networks) to automatically score the phenology of individual specimens, a workflow that has shown much promise (Lorieul et al. 2019). All phenological scores will be associated with their specimen records and therefore be accessible through the CCH2 portal.

GET INVOLVED

Specimen digitization entails a number of activities, such as pre-curation, barcoding, photographing, and image processing, that require a great deal of human participation. Each institution relies on the dedication of faculty, staff, paid and unpaid students (some receiving research credit for their work), and community volunteers to conduct digitization. Many institutions are building partnerships with naturalist and environmentalist groups, such as local chapters of the California Native Plant Society to accelerate the rate of digitization and engage the broader community. For instance, several institutions are crowdsourcing label capture using Notes from Nature, an online platform that engages citizen scientists to transcribe label data from images into designated text fields (notesfromnature.org). The CAP TCN will also collaborate with Notes from Nature to create phenology-themed online "expeditions" in which volunteers use specimen images to score specimens' phenological statuses.

All interested groups and individuals are invited to contribute via online crowdsourcing opportunities and to participate in on-site citizen science events (e.g., the Worldwide Engagement for Digitizing Biodiversity Collections event; wedigbio.org) as they become available. Interested parties also have the opportunity to participate in one of several phenology workshops that will be conducted at UC Santa Barbara, Santa Barbara Botanic Garden, Rancho Santa Ana Botanic Garden, and/or UC Berkeley in 2020–2022. These workshops will expose participants to the importance of phenological observations, the resources available in the CCH2 portal, and native pollinators and native plants, and they will encourage the continuation of current phenological monitoring programs. More information about each of these ways to get involved—Notes from Nature expeditions, on-site digitization events, and phenology workshops—will be posted on the project website (capturingcaliforniasflowers.org).

The CAP TCN further invites all herbaria that are either located in California or can share specimen data representing the California Floristic Province to collaborate with the CAP TCN. Posting and managing data on the CCH2 data portal is an efficient and effective way to improve data quality, share specimen data, and enhance institution visibility, and all are welcome to engage in the CAP TCN project.

CONCLUSION

Capturing images of herbarium specimens is a critical task for mobilizing herbarium specimen data for research and education. Specimen images can provide a wealth of data that characterize the morphology, pathology, and phenology of the plants they represent. The California Phenology Thematic Collections Network will add nearly one million images from the United States' most diverse floristic province to the public sphere. Accompanying these images will be full label data, georeferenced coordinates, and the phenological statuses of the specimens. These data will rapidly enable and inspire research on California's changing flora through integration with the California Phenology Project, the Plant Phenology Ontology, and data generated through other digitization projects. We invite all interested individuals, groups, and herbarium collections to contribute to and benefit from this growing resource.

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CARDUUS CINEREUS (ASTERACEAE) – NEW TO NORTH AMERICA

John F. Gaskin
USDA ARS, 1500 North Central Avenue, Sidney, MT 59270 USA
john.gaskin@ars.usda.gov

Eric Coombs
870 S 2400 W, Logan, UT 84321 USA

Dean G. Kelch
California Department of Food and Agriculture, 1220 N St., Sacramento, CA 95814 USA

David J. Keil
Biological Sciences Department, California Polytechnic State University,
San Luis Obispo, CA 93405 USA

Mark Porter
Oregon Department of Agriculture, 401 NE 1st St., Suite 10, Enterprise, OR 97828 USA

Alfonso Susanna
Botanic Institute of Barcelona (IBB, CSIC-ICUB), Passeig del Midgia s.n.,
Parc de Montjuïc, ES08038 Barcelona, Spain

Abstract

Carduus cinereus M.Bieb. populations have been discovered in the Hells Canyon Wilderness of northeastern Oregon and western Idaho. These plants were initially identified as *C. pycnocephalus* L. They are distinguished from that species by loosely clustered, usually pedunculate, heads and by scarious-margined phyllaries. These plants are genetically distant from other North American *Carduus* species (<94% similarity) based on DNA sequence comparisons of the internal transcribed spacers between the 18S and 26S nuclear rDNA regions. *Carduus cinereus* is new to North America. A revised key to the species of *Carduus* in North America is presented.

Key Words: Asteraceae, *Carduus cinereus*, taxonomy, non-native, invasive species.

Carduus L. comprises about 90 species from Eurasia and northern Africa, mainly in the Mediterranean region (Susanna and Garcia-Jacas 2007). Currently, five *Carduus* species are listed as introduced in North America (Keil 2006). A thistle collected in the Hells Canyon Wilderness in the northeastern corner of Oregon was initially identified by noxious weed managers as *Carduus pycnocephalus* L. (Italian thistle). Over several years, the same thistle was found at additional locations. Identification of the plants was challenged in 2014 by Eric Coombs (then State Biological Control Entomologist for the Oregon Department of Agriculture), who noted morphological differences between populations of *C. pycnocephalus* from southeastern Oregon and the plants that had been identified as *C. pycnocephalus* in northeastern Oregon. Based on morphology and the molecular phylogenetic analysis described below, we conclude that a species new to North America, *Carduus cinereus* M.Bieb., is present in northeastern Oregon and adjacent Idaho.

Taxonomic Treatment

Carduus cinereus M.Bieb., Fl. Taur.-Caucas. 2:270. 1808. *Carduus pycnocephalus* L. subsp. *cinereus* (M.Bieb.) P.H.Davis, Notes Roy. Bot. Gard. Edinburgh 33(3):429. 1975; *Carduus arabicus* Jacq. subsp. *cinereus* (M.Bieb.) Kazmi, Mitt. Bot. Staatssamml. München 5:451. 1964.

Annuals, 15–120 cm tall. **Stems** simple to openly branched, loosely tomentose; winged, teeth of wings to 5 mm long, wing spines to 10 mm long. **Leaves** basal, tapering to winged petioles, blades to 10 cm long, margins pinnately 2–5-lobed, abaxial faces tomentose, adaxial faces loosely tomentose; cauline, sessile, shorter, distally greatly reduced. **Heads** borne singly or clustered in ± loose groups of 2–5 at ends of branches and in distal axils, sessile or short-pedunculate. **Peduncles** 0–3 cm long, unwinged to sparsely winged, tomentose. **Involucres** cylindric to ellipsoid, 12–20 mm long × 7–20 mm in diameter. **Phyllaries** linear-lanceolate, the outer, with appressed, loosely tomentose bases 2–3 mm wide and ascending, linear appendages 0.5–1.0 mm wide, scarious-margined, distally scabrous on faces and margins, spine tips 1–2 mm long, inner, straight, erect, with armed or minutely armed tips. **Corollas** ± purple, 12–15 mm long; lobes ca. 2.5 times longer than throat. **Cypselae** golden brown to brown, 4–6 mm long, finely-nerved; **pappus** bristles 10–20 mm long.

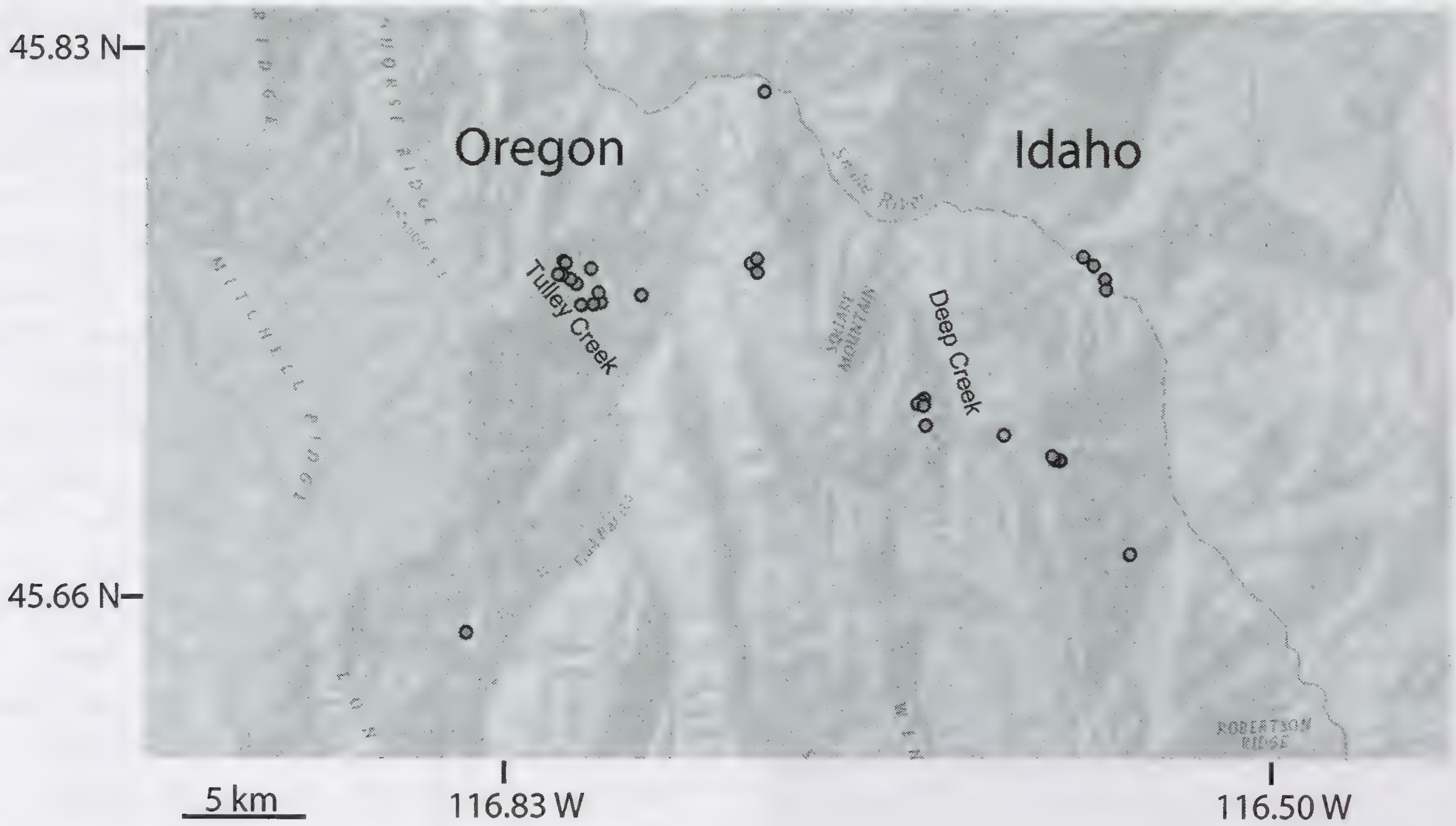

FIG. 1. Map of *Carduus cinereus* locations in northeastern Oregon and adjacent Idaho, USA.

Specimens examined: USA. OREGON. Wallowa Co.: Tyron Creek, Snake River Canyon, 45.6737°, –116.5555°, 1650 m, 26 May 2016, *Mark Porter s.n.* (UC); Tulley Creek, Imnaha Canyon, 45.7582°, –116.7895°, 1650 m, 4 May 2016, *Mark Porter s.n.* (CDA, UC); Idaho. Idaho Co.: Pittsburgh Landing, Snake River Canyon, 45.7653°, –116.5705°, 2500 m, 10 May 2016, *B. Smengut s.n.* (UC);

TAXONOMIC RELATIONSHIPS

Carduus cinereus has been considered to be part of a species complex including *C. arabicus* Jaqu. and *C. pycnocephalus* (Kazmi 1964, Davis 1975). Kazmi (1964) and Rechinger (1979) treated *C. cinereus* as a subspecies of *C. arabicus*. Davis (1975) subordinated both *C. arabicus* and *C. cinereus* within a broadly defined *C. pycnocephalus*. The three taxa involved are closely related. Typical *C. pycnocephalus* from the western Mediterranean and *C. cinereus* from the Eastern Mediterranean and the Irano-Turanian region differ morphologically. Identifying the numerous intermediate forms noted by Davis (1975) is problematic. We treat the three main taxa of the complex as species, as did Tamamschian (1963).

DISTRIBUTION AND ECOLOGY

To date, two relatively large sites are known for *C. cinereus* for North America: Tulley Creek and Deep Creek, Oregon, and satellite populations are known (Fig. 1). We presume that future inventories will reveal a wider distribution of *C. cinereus*. The infested area is a rugged canyon grassland with scattered shrubby and forested areas in a temperate continental climate (Fig. 2A). Local variation in topography and aspect result in a variety of plant community types over small areas. Largely basaltic soils are mixed with ash and Loess deposits and provide a wide variety of substrates that impact plant community distribution. In northwestern North America, *C. cinereus* often occurs in plant communities dominated by native bunchgrasses, including bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve) and Idaho fescue (*Festuca idahoensis* Elmer) (for regional plant community descriptions, see Johnson and Simon, 1987). To date, *C. cinereus* has been found in sites ranging from dry rocky talus on southern aspects to deeper soil in more mesic sites. Reproduction is by seed. Spread is presumed to be by wind and animals.

ORIGIN

When and how *C. cinereus* arrived in northwestern North America is unknown. The area was settled sparsely during the early 19th century; human activities were initially small homesteads. Later agricultural activities centered around sheep grazing, followed in the 1940s by cattle ranching. *Crupina vulgaris* Cass. (common crupina) is also found in the area and it has been postulated that its seed came to the area in sheep fleeces brought by Basque herders (Roché et al., 2003). *Carduus cinereus* is not known from western Europe; a different pathway for its introduction is likely.

METHODS

DNA was extracted from ~10 to 20 mg samples of silica-dried branchlet material from 21 individual plants from Oregon and Idaho (specimen information in Table 1) using a modified CTAB method (Hillis et al. 1996). We sequenced the internal transcribed spacers (ITS 1 and ITS 2) between the18S and 26S nuclear rDNA regions, including 5.8S. We PCR amplified and sequenced using the forward and reverse primers ITS 1 (5′-TCCGTAGGTGAACCTGCGG-3′) and ITS 4 (5′-TCCTCCGCTTATTGATATGC-3′) from White et al. (1990). PCRs were conducted using the thermal

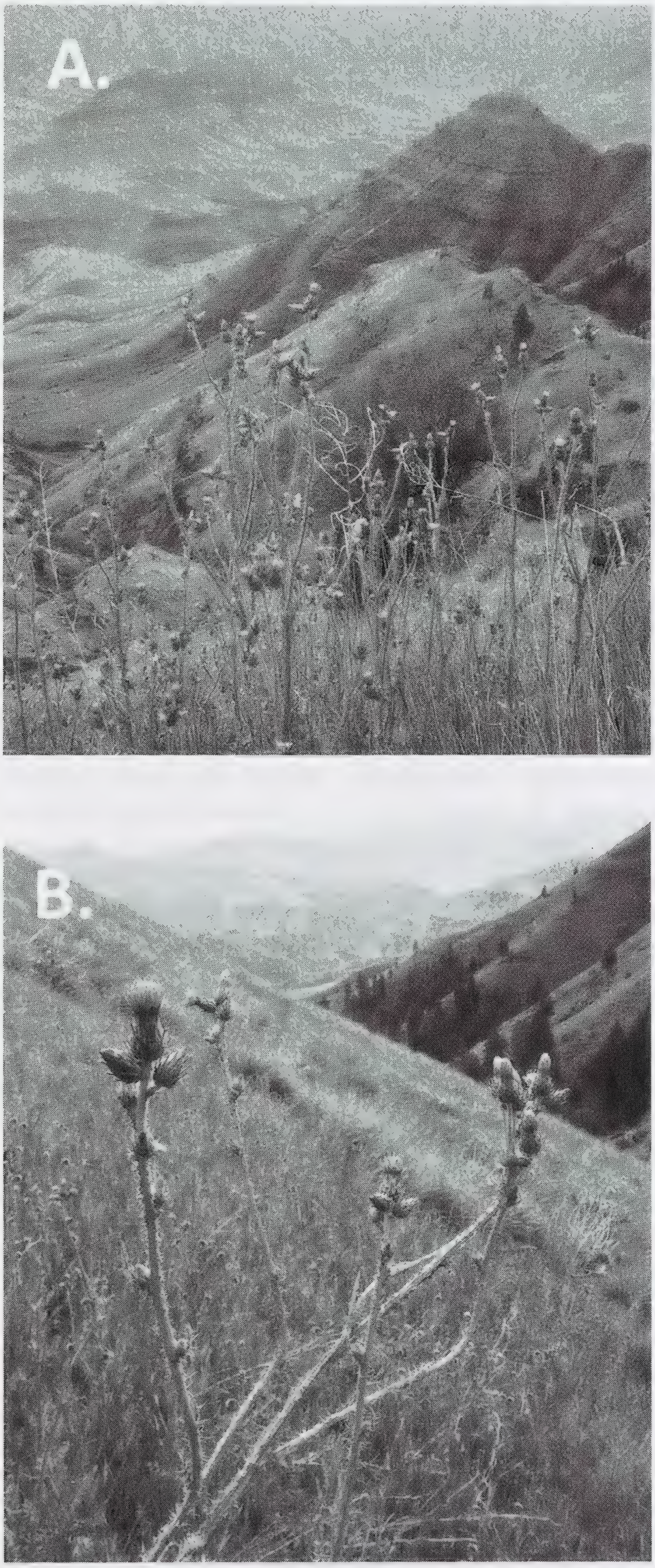

FIG. 2. *Carduus cinereus* found in northeast Oregon, USA. A. *Carduus cinereus* growing in the lower Imnaha region of Hells Canyon near the Idaho border in the rugged and variable topography. B. *Carduus cinereus* inflorescences.

cycling program: one cycle of 120 sec at 95°C, then 30 cycles of 60 sec at 95°C, 60 sec at 54°C, 120 sec at 72°C, and followed by one cycle of 300 sec at 32°C; each 30 μL reaction contained 3 μL of genomic DNA, 3 μL 10X NH_4 PCR buffer (Bioline, Taunton, Massachusetts), 1.5 μL 50 mM $MgCl_2$, 0.24 μL 100 mM dNTP mix, 3 μL 2 μM of each primer, and 0.15 μL (0.75 units) of Biolase DNA Polymerase (Bioline). PCR products were purified using QIAquick Gel Extraction kits (Qiagen, Germantown, Maryland). Our sequence reaction cycling program consisted of one cycle of 60 sec at 96°C, then 25 cycles of 10 sec at 96°C, 5 sec at 50°C, 240 sec at 60°C; each 10 μL reaction contained 1.5–3 μL of PCR template, 3 μL 5X sequence buffer (Thermo Fisher Scientific, Waltham, Massachusetts), 0.85 μL each primer, 1 μL BigDye Terminator Reaction Ready Mix v 3.1 (Thermo Fisher Scientific). Sequencing was performed on an ABI 3130 Genetic Analyzer (Thermo Fisher Scientific). ITS sequences were downloaded from GenBank for other taxa included in the analyses. The analyzed taxa included all *Carduus* species known from North America (*C. acanthoides* Gren. & Godr., *C. crispus* Huds., *C. nutans* L., *C. pycnocephalus*, and *C. tenuiflorus* Curtis), selected *Carduus* species not found in North America (*C. defloratus* L., *C. personata* Jacq., *C. carlinoides* Steud., and *C. tmoleus* Boiss.), putative *C. cinereus* from Oregon and Idaho, USA, plants from Oregon morphologically identified as *C. pycnocephalus* and *C. tenuiflorus*, and outgroup species from *Cirsium*, *Onopordum*, and *Centaurea*. Sequences were aligned using ClustalW in MEGA 6.05 (Tamura et al. 2007). Genetic distance between each accession and a maximum likelihood tree with 1000 bootstraps (using a General Time Reversible model) were constructed in MEGA 6.05. Missing nucleotide sequence data from GenBank accessions were coded as N. Insertion/deletion events were included in the analysis. Within *Carduus*, there were two single base pair insertion/deletion events.

RESULTS

The ITS region provided 637 alignable base pairs. There were 22 nucleotide sites (22/637 = 3.4%) in which the USA *C. cinereus* contained alleles not found in other *Carduus* from North America. The maximum likelihood tree (Fig. 3) separated the USA *C. cinereus* from all other North American *Carduus* taxa with 99% bootstrap support. The pairwise genetic distance between the USA *C. cinereus* and all North American *Carduus* taxa ranged from 3.9–4.9%, as compared to a maximum distance of 2.9% between known *Carduus* in North America. The pairwise genetic distance between *C. pycnocephalus* (perhaps the closest North American match to the USA *C. cinereus* morphologically) and the USA *C. cinereus* was 4.9%. The genetic distance between *Carduus* taxa and the closest outgroup (*Cirsium vulgare*) was 4.3–5.8%; the genetic distance between the USA *C. cinereus* and the closest outgroup (*Cirsium vulgare*) was 5.9%. The GenBank accession number for our *C. cinereus* collections (all have identical ITS DNA sequences) is MK253665. There were no *C. cinereus* ITS sequences in GenBank; we could not make a genetic distance comparison with ITS sequences obtained from conspecific specimens. There were "*C. pycnocephalus* subsp. *arabicus*" and *C. pycnocephalus* subsp. *albidus* (M.Bieb) Kazmi

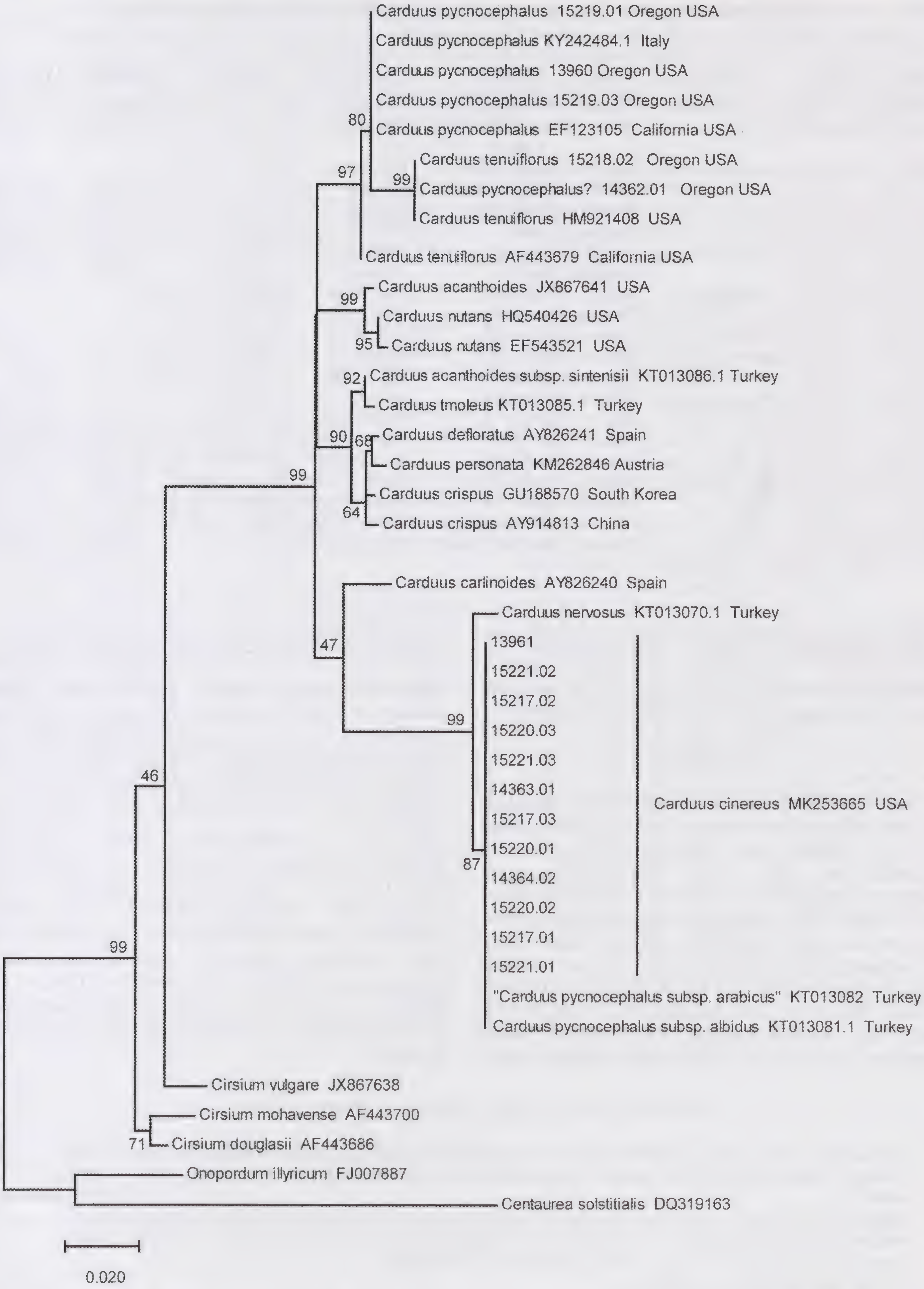
Carduus pycnocephalus 15219.01 Oregon USA
Carduus pycnocephalus KY242484.1 Italy
Carduus pycnocephalus 13960 Oregon USA
Carduus pycnocephalus 15219.03 Oregon USA
80
Carduus pycnocephalus EF123105 California USA
Carduus tenuiflorus 15218.02 Oregon USA
97
99
Carduus pycnocephalus? 14362.01 Oregon USA
Carduus tenuiflorus HM921408 USA
Carduus tenuiflorus AF443679 California USA
Carduus acanthoides JX867641 USA
99
Carduus nutans HQ540426 USA
95
Carduus nutans EF543521 USA
92
Carduus acanthoides subsp. sintenisii KT013086.1 Turkey
Carduus tmoleus KT013085.1 Turkey
90
68
Carduus defloratus AY826241 Spain
Carduus personata KM262846 Austria
99
Carduus crispus GU188570 South Korea
64
Carduus crispus AY914813 China
Carduus carlinoides AY826240 Spain
Carduus nervosus KT013070.1 Turkey
47
13961
15221.02
15217.02
99
15220.03
15221.03
46
14363.01
Carduus cinereus MK253665 USA
15217.03
15220.01
87
14364.02
15220.02
15217.01
99
15221.01
"Carduus pycnocephalus subsp. arabicus" KT013082 Turkey
Carduus pycnocephalus subsp. albidus KT013081.1 Turkey
Cirsium vulgare JX867638
Cirsium mohavense AF443700
71
Cirsium douglasii AF443686
Onopordum illyricum FJ007887
Centaurea solstitialis DQ319163
0.020

FIG. 3. Maximum likelihood tree of *Carduus* and outgroups for the internal transcribed spacer of 18S to 26S nuclear rDNA region. Accession information includes genus, species, GenBank accession number or our DNA number, and geographic origin, if known. Bootstrap values are posted next to branches.

TABLE 1. Accession Information for DNA Samples of *Carduus* Species from Oregon and Idaho, USA.

DNA sample #	Genus	Species	State	Location	Nearest town or river	Site code	Latitude	Longitude
13960	*Carduus*	*pycnocephalus*	Oregon	Douglas County	Winston		43.0965	−123.3889
13961	*Carduus*	?	Oregon	Lower Imnaha Canyon	Imnaha		45.7582	−116.7896
14362.01	*Carduus*	*pycnocephalus?*	Oregon	North Bank Rd.	Roseburg			
14363.00	*Carduus*	?	Oregon	Tulley Creek Site	Imnaha		45.7582	−116.7896
14364.00	*Carduus*	?	Oregon	Holmes Site	Imnaha		45.7685	−116.7186
15217.01	*Carduus*	?	Oregon	Tryon 1	Imnaha	Tryon 1	45.7046	−116.5878
15217.02	*Carduus*	?	Oregon	Tryon 2	Imnaha	Tryon 2	45.7046	−116.5878
15217.03	*Carduus*	?	Oregon	Tryon 3	Imnaha	Tryon 3	45.7046	−116.5878
15218.01	*Carduus*	*tenuiflorus*	Oregon	Dixonville	Dixonville	CATE-1		
15218.02	*Carduus*	*tenuiflorus*	Oregon	Dixonville	Dixonville	CATE-2		
15218.03	*Carduus*	*tenuiflorus*	Oregon	Dixonville	Dixonville	CATE-3		
15219.01	*Carduus*	*pycnocephalus*	Oregon	Dixonville	Dixonville	CAPY-1		
15219.02	*Carduus*	*pycnocephalus*	Oregon	Dixonville	Dixonville	CAPY-2		
15219.03	*Carduus*	*pycnocephalus*	Oregon	Dixonville	Dixonville	CAPY-3		
15220.01	*Carduus*	?	Idaho	Cat Creek	Snake River	P. snake 1	45.7657	−116.5705
15220.02	*Carduus*	?	Idaho	Cat Creek	Snake River	P. snake 2	45.7657	−116.5705
15220.03	*Carduus*	?	Idaho	Cat Creek	Snake River	P. snake 3	45.7657	−116.5705
15221.01	*Carduus*	?	Oregon	Tulley Creek 1	Tulley Creek	Tulley Creek 1	45.7582	−116.7896
15221.02	*Carduus*	?	Oregon	Tulley Creek 2	Tulley Creek	Tulley Creek 1	45.7582	−116.7896
15221.03	*Carduus*	?	Oregon	Tulley Creek 3	Tulley Creek	Tulley Creek 1	45.7582	−116.7896
15837.00	*Carduus*	*crispus*	Oregon	Wallowa County	Enterprise		45.3948	−117.2994

GenBank accessions collected by S. Kostekci and T. Arabaci from Turkey; these had a 0.3% genetic distance from our USA *C. cinereus*. These taxa may prove to be conspecific with the USA *C. cinereus*.

DISCUSSION

If our USA *C. cinereus* with the distinct morphology were a hybrid of existing *Carduus* already found in North America, one would expect that the ITS sequence from such a recent hybridization event might not be subject to concerted evolution (Elder and Turner 1995) and would contain heterozygotic loci (or nucleotide additivity patterns) where there are sequence differences between the two parental taxa. We found only 2/637 loci (0.3%) in the USA *C. cinereus* that were heterozygotic, and only one of these loci showed multiple alleles within North American *Carduus*. In addition, the presence in the USA *C. cinereus* of alleles unique to sampled North American *Carduus* renders its origin as a recent interspecific hybrid unlikely. The minimum genetic distance of USA *C. cinereus* from any *Carduus* listed as present in North America (3.9%), compared to the maximum genetic distance between all other North American *Carduus* species (2.9%) suggests that this is a distinct taxon. Our collections differ morphologically from *C. pycnocephalus* in North America by having heads usually pedunculate and loosely clustered (Fig. 2B) vs. usually sessile and tightly clustered and phyllaries scarious-margined vs. not scarious-margined. Given the differences in morphology and DNA sequence between *C. pycnocephalus* subsp. *pycnocephalus* and our collections from Oregon and Idaho, we suggest that we have found a species new to North America, and identify it as *C. cinereus* M.Bieb.

MODIFIED KEY TO *CARDUUS* SPECIES IN NORTH AMERICA

1. Phyllaries 2–7 mm wide, usually wider than the appressed bases; peduncles often elongate, distally wingless; heads often nodding, usually borne singly or in leafy corymbiform arrays; involucres 20–70 mm diam . . . . *Carduus nutans*

1′ Phyllaries 0.5–2.0 mm wide, usually narrower than the appressed bases; peduncles short, if present, usually winged throughout, less often sparsely winged or unwinged; heads erect, 1–many, often clustered or loosely clustered at branch tips or upper axils; involucres 7–30 mm diam

  2. Involucres spheric or hemispheric

    3. Corollas 13–20 mm long; heads 18–25 mm long; involucres 14–20 mm long; abaxial leaf faces glabrate except for long, curled, septate hairs along veins . . . . *Carduus acanthoides*

    3′ Corollas 11–16 mm long; heads 15–18 mm long; involucres 12–17 mm long; abaxial leaf faces sparsely to densely tomentose with fine, non-septate hairs and often with curled, septate hairs along veins as well . . . . *Carduus crispus*

  2′ Involucres cylindric or narrowly ellipsoid

4. Heads 5–20 at ends of branches; phyllaries glabrous or sparingly tomentose, distally ciliolate or glabrous . . . . *Carduus tenuiflorus*
4′ Heads 1–5 at ends of branches; phyllaries ± persistently tomentose, distally scabrous on margins and faces
5. Heads usually pedunculate and loosely clustered; phyllaries scarious-margined . . . . *Carduus cinereus*
5′ Heads usually sessile and tightly clustered; phyllaries not scarious-margined. . . . . . *Carduus pycnocephalus*

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BIOLOGY OF THE EPHEMERAL GEOPHYTE, STEER'S HEAD (*DICENTRA UNIFLORA*, PAPAVERACEAE) IN THE SOUTHERNMOST CASCADE RANGE, BUTTE COUNTY, CALIFORNIA

ROBERT A. SCHLISING
Department of Biological Sciences, California State University, Chico, CA 95929
rschlising@csuchico.edu

HALKARD E. MACKEY, JR.
Retired Environmental Scientist, 3244 Mystery Run, Chico, CA 95973

ABSTRACT

Dicentra uniflora Kellogg (Papaveraceae), a small, single-flowered, ephemeral geophyte, was studied at three main and several secondary forest sites at the southern end of the Cascade Range in California (2009–2018). Emergence was closely linked to snowmelt, with flowering to senescence taking six to seven weeks, at elevations ranging from 1350–2575 m. Plants transitioned from flowering to fruit maturation within three weeks. Percent seed set in this perennial was high, ranging from 81–93% over five sites; seeds per fruit ranged from 44–83. In 2018, weekly field observations quantified the fate of flowers on plants staked when flowers appeared: only 27–43% of the flowers produced mature fruits with seeds, 23–24% dried up, and 25–30% disappeared, often leaving the pedicels. Black-tailed deer are suspected to be the primary herbivore, although nocturnal larvae of the butterfly *Parnassius clodius*, known to consume *Dicentra* leaves, may also be responsible at higher elevations. Each seed bears an easily-dislodged elaiosome, but little of the expected seed dispersal by ants was seen throughout the study. Field plantings of seeds illustrated that germination can occur in winter, below the snow, with seedlings bearing only a single cotyledon emerging from the ground in the spring. A seedling quickly produces a tiny food-storing, belowground bulblet before disappearing with the summer drought of the Mediterranean-type climate. The second-year plant produces a new bulblet and sometimes a tiny tuber, but only a single leaf, and plantings in the field suggest that it may take up to 10 years or more before an individual reaches flowering stage. A flowering plant has one or two fusiform tubers approximately 21 mm long and a cluster of ∼9 whitish bulblets approximately 4 mm long. Published research in the closely-related *D. cucullaria* (L.) Bernh. indicates that bulblets are undeveloped food-storage leaf bases unique to four species of *Dicentra*, capable of giving rise to small plants and providing food for plant development. Bulblets planted in this field study clearly indicate they are capable of asexual reproduction. As in some other geophytes, dry weight of *D. uniflora* tubers was significantly greater in June at the beginning of the summer drought than in November when the plants began renewed root growth early in the fall wet season. The depth to the tops of tubers on plants occurring in clusters varied from 3.2–10.7 cm in the rocky, loamy or sandy-loamy soils of these sites.

Key Words: bulblet, *Dicentra uniflora*, elaiosome, geophyte, high seed set, *Parnassius clodius*, phenology, tuber.

When in flower, the steer's head, *Dicentra uniflora* Kellogg (Papaveraceae) (Fig. 1A) attracts photographers and plant collectors. Local floras often note that this species flowers soon after snowmelt, but the rest of the life cycle of this small plant is not well known. Literature on its ecology is very limited, even though this species has a wide geographic range, from southern British Columbia, south to the North Coast Ranges and the Sierra Nevada, CA, and east and south to the mountains of Montana, Wyoming and Utah (Stern 1997). This species was included as characteristic of a snowbed plant community in the western Cascades in Oregon (Hickman 1976).

This ephemeral perennial, about 3-7 cm tall, is the smallest of the 20 species in the genus *Dicentra* Bernh. (Stern 1997). One or two dissected leaves and a single flower appear annually, and the entire plant disappears aboveground, as it senesces in six to seven weeks. The term "geophyte" has apparently not been applied to this species, although its quick drying down to the tuber after the wet season, is consistent with that life form (Dafni et al. 1981; Rundel and Anderson 2016). Most reports on geophytes focus on monocotyledonous plants (e.g., Rundel 1996), not on dicotyledonous species such as *D. uniflora*. This species is acaulescent, and descriptions in floras often indicate the plants have a cluster of whitish bulblets at the top of the tubers (Stern 1997; Baldwin et al. 2012). A detailed morphogenesis study on four species of *Dicentra* by Walton and Hufford (1994) helps explain the complex belowground organs of this species and emphasizes the asexual role of the bulblets. The monograph of *Dicentra* (Stern 1961) provided extensive morphological and anatomical data and included a phylogeny for the genus.

Some ecological information was provided by Berg (1969) involving the elaiosomes and carriage of the seeds by ants. A recent report covered some features of habitat and reproductive biology for the *D. uniflora* in British Columbia (Courtney and

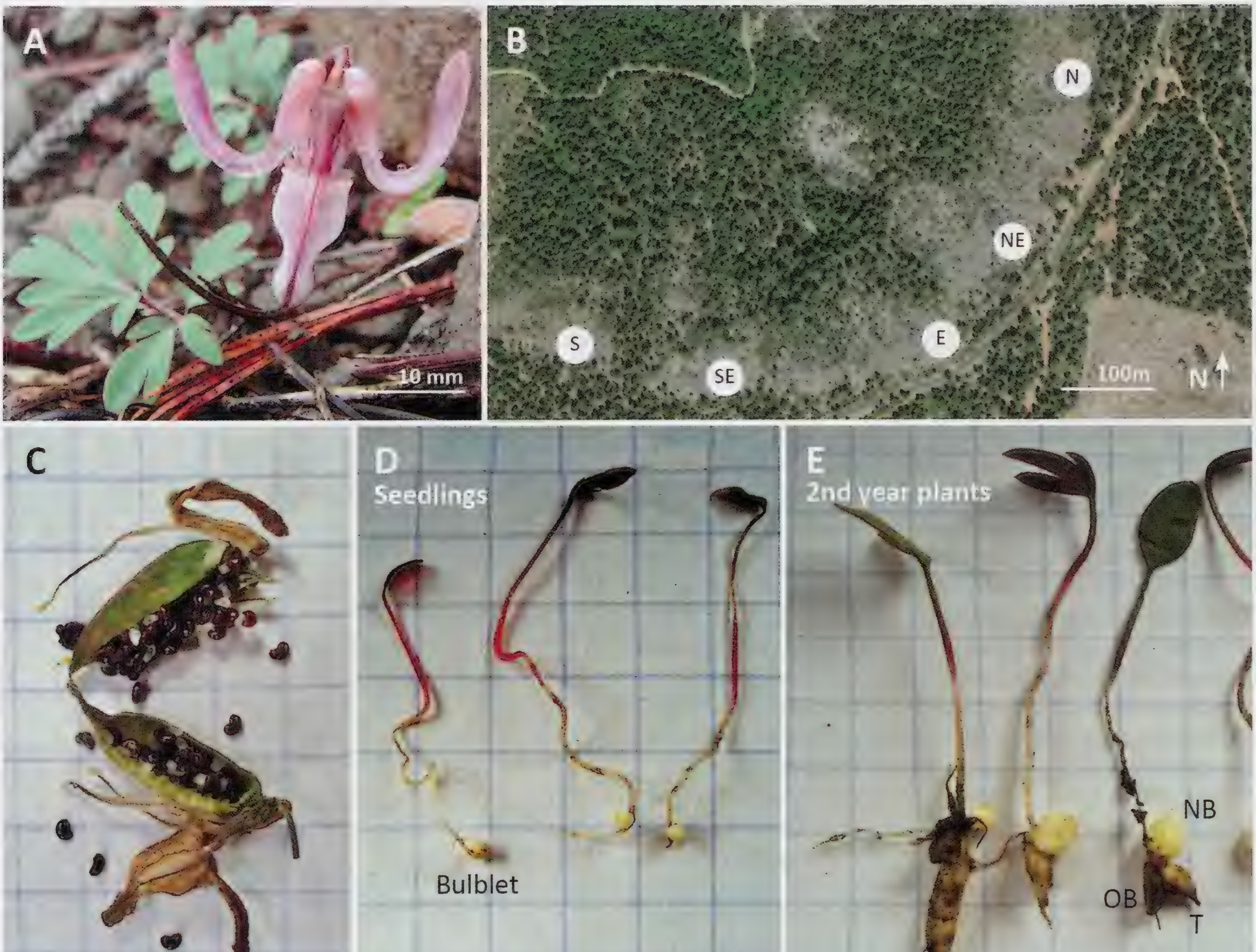

FIG. 1. Biology of *Dicentra uniflora*. A. Plant with single flower (photograph by Robert D. Fischer). B. Aerial view (from Google Earth) of the Tuscan Formation outcrop "crescent" on Carpenter Ridge, Butte County. The five study areas in open coniferous forest adjacent to the steep rock outcrop are indicated by letters N, NE, E, SE, and S. The USGS benchmark is located in study area E at 4535 ft (1383 m) elevation. C. One split-open fruit, showing several of the small, whitish elaiosomes visible against the black seeds (5 mm grid). D. Seedlings, with small bulblets on the underground portions (5 mm grid). E. Second-year plants, each with a brownish old (spent) bulblet (OB), a new cream-colored bulblet (NB), and a small tuber (T) (5 mm grid). F. Mature tubers, showing cluster of bulblets attached to the condensed stem axis at the top of two fresh tubers and two old, desiccated tubers. New roots were emerging on this plant when collected on 5 November 2010. G. Caterpillar of *Parnassius clodius*, a probable herbivore on *D. uniflora* leaves and fruits at the higher elevation study sites. Collected at the Summit study site. H. Adult butterfly, *Parnassius clodius*, also collected at the Summit study site. These distinctive butterflies indicate the larval stages are likely present as herbivores on *Dicentra* species in an area.

Scotter 2018), and the biology was briefly described for the species in Utah (Rayl 2002). In January 2019, at the 9th Symposium of the Northern California Botanists, the authors presented the first descriptions of the growth patterns observed from field plantings of seeds and bulblets, as well as survival of flowers and fruits at varied elevations ranging from 1350 to 1940 m. *Dicentra uniflora* is listed as one of the larval food plants for a species of butterfly, *Parnassius clodius* Ménétriés, Papilionidae (Scott 1986; Pyle 2002; Shapiro and Manolis 2007; James and Nunnallee 2011). Diane Debinski (Montana State University, personal communication) and her colleagues (e.g., Aukland et al. 2004) have focused on the plant as host to the butterfly larvae and its relation to climate change in Montana.

After this species was collected at Butte County sites in the southernmost Cascade Ranges of California in the spring of 2009 (Appendix 1), a search for published information indicated there was very little known about the biology of the plant. The purpose of this field study was to elucidate/describe features of the entire life cycle of *D. uniflora*. The major goal was to document its overall phenology by examining the plant in several sites at different elevations within a limited region over several years. Within this phenological context, several of the most important questions we wanted to answer were: 1) how similar are the times of emergence, reproduction and senescence in different years, 2) how successful are the plants at producing seeds, 3) when and where do seeds germinate, and 4) what is the timing and pattern of growth of the seedlings, bulblets, and tubers? This report presents results from the first part of our long-term field studies on *D. uniflora*.

MATERIALS AND METHODS

Study Sites

To incorporate potential variation from the plants in the southernmost Cascade Range, three main study sites in northeastern Butte County were used (Appendix1). Additional observations were made in another Butte County site (Humboldt Peak) and at Lassen Volcanic National Park (LVNP). Bedrock for all Butte County sites is Tuscan Formation volcanic mudflow. Soils in the three Butte County sites are rocky, and consist of sandy loam or loam, as determined with separate composite soil samples taken for each site in 2009 and sent to A. & L. Analytical Laboratories, Inc., Memphis, TN (Kannely and Schlising 2014).

All study sites have a Mediterranean-type climate, with a shorter winter-wet season at the lowest site than at the other sites. The lowest site (Carpenter Ridge) has a weather-recording station about 1.7 km distant, and at an elevation of 1735 m, or 350 m higher, from which climatic measurements were available for 2008–2018 (CA Department of Water Resources 2018a). Precipitation and temperature data from this source were used to approximate conditions for Ridge and the other main sites in Butte County. Another study site (Humbug Summit) had snowfall data available for 2008–2018 (CA Department of Water Resources 2018b). Snowfall and rainfall data for LVNP study site (Brokeoff Trail) were obtained for 2008–2011 (CA Department of Water Resources 2018c,d).

Three main study sites. The three main study sites, at different elevations, were visited frequently in spring and early summer during the entire, short aboveground cycle of this ephemeral geophyte. Secondary sites were visited less frequently to provide supplemental information.

Ridge.—The lowest main study site, Carpenter Ridge, or "Ridge," is about 6.9 km southwest of Butte Meadows, at 40° 03′ 19.9″ N, 121° 35′ 40.1″ W, and has a USGS benchmark at 1383 m elevation at its center. *Dicentra* plants were studied in five disjunct areas on or near the top of Ridge, differing in elevation by no more than 30 m. Main forest trees are *Pinus ponderosa* Lawson & C.Lawson, *P. lambertiana* Douglas, *Pseudotsuga menziesii* (Mirb.) Franco, *Calocedrus decurrens* (Torr.) Florin, *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr., and *Quercus kelloggii* Newb.; shrubs include *Ceanothus integerrimus* Hook. & Arn. and *Arctostaphylos patula* Greene (Kannely and Schlising 2014). Soils in all five areas are sandy loams, with percent particles ranging from 60.8 to 74.7 (sand), 17.2 to 29.4 (silt), and 5.4 to 9.7 (clay).

The five areas at Ridge extend over a length of about 805 m, and vary from each other in exposure and slope, and are named according to their position on the major "crescent" formed here by Carpenter Ridge (Fig. 1B). Ridge N is the area farthest north; it is unshaded and has the most southerly exposure (WNW). Few herbaceous plant associates were in flower with *Dicentra*, mainly *Sanicula tuberosa* Torr. and *Microsteris gracilis* (Douglas ex Hook.) Greene—two associates known at all five study areas here. Ridge NE, farther to the south, has some shade from trees and a sprinkling of pine needles on the ground. Flowering associates include *Allium campnulatum* S.Watson, as well as the *Sanicula* and *Microsteris*, and has an exposure to the NW. Ridge E (with the USGS benchmark) is unshaded, with the associates mentioned, as well as *Hemizonella minima* A.Gray, and has a NNW exposure. Ridge SE is shaded part of the day. Additional associates include *Castilleja applegatei* Fernald subsp. *pinetorum* (Fernald) T.I.Chuang and Heckard. It has an exposure to the north. Ridge S, the southwestern-most area, has only the upper part shaded and exposure is to the north. Flowering associates are mainly *Sanicula*, *Microsteris* and *Hemizonella*. The loamy soil here has the lowest percentage of clay particles (5.5%) and the highest percentage sand particles (74.7%) of the five areas studied and has sparse litter. The Mediterranean climate results in most precipitation falling from mid-October to mid-May. Snow melts first at Ridge N and last at Ridge S each spring.

Meadow.—The second main study site, "Meadow," is located 6.6 km east of Jonesville, and 0.3 km south of the road along Scotts John Creek, on U.S. Forest Service road 26N27, at 40° 06′ 21.0″ N, 121° 25′ 35.40″ W, and 1746 m elevation (Kannely and Schlising 2014). *Dicentra uniflora* grows mainly in a zone between dense forest trees and a wet meadow, and in an adjacent open, drier meadow. Some plants receive shade from trees during flowering, others are not shaded; aspect is to the northwest. Trees are mostly *Abies concolor* and *Pinus jeffreyi* Balf.; shrubs include *Symphoricarpos mollis* Nutt. and *Ribes roezlii* Regel. Early-flowering herbaceous associates are *Hackelia californica* (A.Gray) I.M.Johnst., *Allium campanulatum*, *Collinsia torreyi* A.Gray var. *wrightii* (S.Watson) I.M.Johnst., and *Dicentra pauciflora* S.Watson. *Dicentra formosa* (Haw.) Walp. is also common in the surrounding forest. Soil is a loam (50.8% sand, 35.4% silt, 13.7% clay); litter from trees occurs primarily on *Dicentra pauciflora* and *D. formosa* plants. This site, 360 m higher than Ridge, has snow persisting longer. In all years of the study, snow on the local unpaved roads prevented spring observations until late May or early June.

Summit.—The third main study site, "Summit," occurs on Humbug Summit Road, 1.5 km south of Humbug Summit, at 40° 6′ 20.6″ N, 121° 23′ 27.7″ W, and 1945 m elevation, 560 m higher than Ridge. *Dicentra uniflora* was studied on a small, open slope facing the southwest, in a forest of red fir (*Abies magnifica* A.Murray bis) and some *Pinus contorta* Douglas ex Loudon subsp. *murrayana* (Grev. & Balf.) Critchf., where the plants receive at least some shade daily during the reproductive season. Main associates flowering with *Dicentra* include *Hackelia nervosa* (Kellogg) M.Johnst., *Allium campanulatum*, and *Collinsia torreyi* var. *wrightii*. Soil is a sandy loam (60.8% sand, 29.4% silt, 9.6 % clay); there is more conifer litter on the soil than at the other two sites. The climate here is similar to that of the Meadow site, with an additional one to two weeks for final snowmelt in this shaded study site. This site was typically not accessible until early or mid-June.

Secondary study sites. Humboldt Summit.—Short segments of the Pacific Crest Trail in northern Butte County east and west of the Humboldt Summit Road were visited on 15 June 2009. Mature fruits from two populations of *D. uniflora* were located at 500 m west of the parking area at approximately 2050 m in elevation in semi-open areas with loose rocky soils (Janeway 2019).

Lassen Volcanic National Park.—Brokeoff Trail was surveyed several times during the spring and summer of 2009 and 2010. The trail begins near Highway 89 and ends at the summit at 2815 m. Populations of *D. uniflora* were observed at 15 locations beginning near the lower portion of the trail at 2065 m to the timber line at 2575 m. Mature fruits were collected in both years, from large populations along lower Brokeoff Trail 40° 25′ 46.73″ N, 121° 32′ 26.00″ W, at 2100 m, and along mid-Brokeoff Trail 40° 26′ 5.27″ N, 121° 32′ 49.78″ W, at 2240 m. The lower site is more forested and less open, and *Claytonia lanceolata* Pursh flowers occurred frequently with *Dicentra*. Hickman (1976) also noted that *C. lanceolata* was an associate of *D. uniflora* in Oregon.

Vegetation Transects

To understand the habitat where *D. uniflora* grows in the Butte County sites, transects were laid out in 2009 and 2010. Ten 1-m^2 plots were established one m apart along each of the 21-m transects at each of the main study sites. In each of the 1-m^2 plots the following were recorded: the number of single, bi-lobed, and tri-lobed leaves; the total number of leaves; the number of leaves in clusters; the numbers of flowers or fruits; and the soil depth within any clusters of *D. uniflora* plants. The 1-m^2 plots were then sub-divided into 0.25-m square sections and data were collected on soil depth in cm at the center of each, by pushing a soil thermometer until resistance in the soil (i.e., rock or bedrock) stopped it in the very shallow soils. Plots were surveyed on Carpenter Ridge as follows: in 2009 (at S on 17 May); in 2010 (at E on 3 May, at N on 13 May, and at SE and S on 22 May). Plots were surveyed at Meadow and Summit on 11 June 2009 and 8 July 2010. During each site visit air and soil temperature data were collected.

Phenology

Historical. Data were reviewed for *D. uniflora* for northern California from the online database of the Consortium of California Herbaria (accessed 2009) and specimens were examined at the Herbarium at California State University, Chico, CA (CHSC). The area of interest (representative of the southernmost Cascade Range) was bounded by latitude north (N) and longitude west (W) as follows: 41° 0′ 0″ N, 123° 0′ 0″ W; 41° 0′ 0″ N, 120° 45′ 0″ W; 39° 25′ 0″ N; 20° 45′ 0″ W; 39° 25′ 0″ N, 123° 0′ 0″ W. Records were found from 1899 to 1998. Elevations ranged from approximately 1200 to 3200 m. Only those records from herbarium sheets with mature pink flowers and that had a clearly identifiable location and elevation were used. Plots of collection date versus elevation were developed to estimate changes in flowering phenology. The most notable features observed were the mature pink flowers and well-developed leaves.

Present-day study sites (2009-2018). The phenology of *D. uniflora* was evaluated at sites in northern Butte County in 2009—2011, 2017, and 2018, and for LNVP in 2009 and 2010. Each site was visited at approximately weekly intervals in the early spring after snowmelt. Sites were systematically walked to record the occurrence of early emergent leaves, flower buds, changes in flower color, fruit development, and senescence. Flowers were marked weekly in 2018 at the Butte County sites to better understand the timing, development, and fate of flowers and fruits. Fruits were considered mature once they had become brown, firm and plump. Only mature fruits were collected for seed counts. Observations of any indications of herbivory, disappearance of flowers or fruit (i.e., free-standing pedicels), non-matured fruits, chewed fruits, and dehiscent fruits were recorded. Senescence of leaves was indicated by a change in color from green to yellow, and finally brown. Changes in weather events, such as late snows, were recorded. Sites were monitored for four to seven weeks at a given elevation. Lower elevation sites were available in April until mid-June. Higher elevation sites were surveyed in June or early July.

When possible, some plant traits were measured systematically every meter along transects. But in years when there were few plants available, as many plants as could be found throughout the entire sample area had to be used. Main features measured were those that characterized growth and could be easily measured or assessed in the field or laboratory.

Reproductive Success

In 2018, small wooden stakes (Bamboo Paddle Picks, 11.4 cm long, Tablecrafts Products Company, Gurnee, IL) were inserted in the soil about five cm upslope from plants with flowers at the three main study sites. To determine how long individual flowers last and the timing of fruit and seed production, stakes were numbered with the week they were used to indicate new (pink) flowers. Weekly changes of these individual flowers were recorded, as from pink to brown, and then to plump/mature fruits before the seeds were lost (Fig. 1C). Stakes were removed as mature fruits were collected individually into #1 coin envelopes (Swinton Avenue Trading, Boca Raton, FL) for study in the laboratory. "Reproductive success" was scored as 1) flower had produced seeds, 2) flower had dried without producing seeds, or 3) the flower or developing fruit was entirely missing by the time the plant senesced.

Features of ovules and seeds. In the laboratory, fruits were examined with dissecting microscopes to count mature seeds versus aborted ovules, to determine ovules per ovary, seeds per fruit, and percent seed set. Seeds were counted as mature if they were black or very dark brown. Weights of the mature seeds were determined in 2009 by weighing 10 batches, each of 25 black seeds with their elaiosomes from fruits collected at Ridge in May. Similarly, 10 batches, each of 25 black seeds with their elaiosomes removed, were weighed to determine separate mean seed and mean eliaosome weights. To determine features of seed germination and the nature of seedlings (e.g., presence of bulblets and tubers), bulk and individual seed plantings were done.

Seed germination—bulk plantings. Batches of 50 seeds each were planted in the five areas at Ridge (15 July 2009 and 4 November 2010), and at Meadow and Summit (2 July 2009), before the fall rains began. Seeds were from fruits collected at the three main sites including each of the five areas at Ridge. Flat spots 30 × 30 cm had the soil loosened to about five cm, had four shallow furrows made, and had four v-creased strips of non-inked newspaper 20 cm long tucked into them to permit finding the seeds later. The strips were lightly sprayed with water, and each had 50 seeds spread along it before 1-1.5 cm of loose soil was spread over the entire planting and covered with a square of 0.25 inch hardware cloth secured with wire loops at the corners. Similar methods had been successfully used to germinate a geophyte with similar-sized seeds at the Ridge site (Kannely and Schlising 2014). Also, measurements of single-leaved seedlings of *D. uniflora* ($n = 19$) averaged 2.8 cm from soil surface to the belowground bulblets (made at the Brokeoff study site), which indicated using these depths were a reasonable approach for our initial field germination studies. These plantings received only natural precipitation. Rows of seeds in their supporting newsprint were recovered at intervals and examined in the laboratory.

Seed germination—individual seed plantings. On 6 July 2009, three plantings of 100 seeds of *D. uniflora* were made on Carpenter Ridge at E, SE, and S. Individual seeds were planted approximately 2.5 cm deep in 10 parallel rows, spaced five cm apart and with five cm spacing between each row. A pair of wooden toothpicks marked the end of each row. All sites had slopes of less than 5% and were cleared of small stones and larger pieces of woody debris. Corners were marked with small stones and each plot was photographed. Seeds planted at these three sites were from fruits collected earlier in the spring of 2009. Seeds were also planted at Ridge NE and N later on 13 July 2009. On 10 August 2009, individual seed plantings were also done at Meadow and Summit in the same manner as for the Ridge sites.

Counts of germinated seeds were made at weekly periods in the spring and early summer of 2010. Locations of germinated seeds were easy to recognize from the locations of the toothpicks, the regular spacing of the plantings, and the small cotyledons (Fig.1D) observed when the seeds germinated. Similar individual plantings were done in 2010. Seedling lengths (including cotyledons), as well as underground parts (as shown in Figs. 1D through 1F) were measured with calipers (General 152 mm Dial, General Tools and Instruments, Secaucus, NJ).

Tubers and Associated Bulblets

To elucidate the nature of the underground parts, entire plants were sampled at Ridge twice in 2010. The first sample was made 12 June, at the end of the wet season, when tubers were expected to be at maximum size/weight because of recent photosynthesis by the leaves (Fig. 1F). Tubers were washed in the laboratory to remove soil, dried, and gently brushed to complete soil removal. Cleaned tubers were further prepared by shaving off the caudex (top area of attachment of other parts) before measuring maximum diameter and length to the nearest 0.1 mm with calipers. Fresh weight was determined on a standard Mettler balance. Tubers were dried in an herbarium plant-press drier at 43°C for three months before re-weighing to determine dry weight.

The second sample was made on 4 November, at the end of the dry season, of plants that had been staked at Ridge S on 12 June so they could be relocated. The ellipsoid bulblets (Fig.1F) at the tops of the tubers were counted, removed from the plants, and combined together in a Petri dish. The whole set of bulblets were spread in a line and every 5th bulblet was sampled and cleaned of soil. The maximum diameter and length of each bulblet were measured to the nearest 0.1 mm. Dry weight was determined after drying for 11 weeks. The tubers bearing these bulblets were treated as with the June sample of tubers: cleaned, shaved at the top, weighed, dried, and re-weighed.

Statistical Analyses

Number of mature seeds per fruit (averaged for several years at each site) were compared across the three main sites (including three areas of the areas at Ridge), using a one-way ANOVA, followed by Tukey post-hoc tests. Seed set at these sites over four years were compared using a two-way ANOVA. Tuber dry weights and also maximum diameters were compared between samples collected before and after the hot, dry summer season using Student's t-tests. Linear regression of elevation versus day of the year (DOY) were used to compare herbarium collections of *D. uniflora* to determine pattern in the flowering phenology of this species in the region of this study. Data were analyzed using RStudio Statistical Computing (RStudio, Inc., Boston, MA).

RESULTS

The principal years showed different patterns of rainfall and snowfall, which influenced the phenological schedule of *D. uniflora* at all sites. Weekly visits to the sites as soon as they became accessible indicated how tightly the first emergence of *D. uniflora* is linked to snowmelt. The first leaves and flower buds were almost always visible as soon as the snow cover was lost and usually even as patches of snow still remained in protected places. Snowfall and rainfall patterns are typical of the northern California Mediterranean-type climate and summarized in Table 1. Snowfall data are not available for Carpenter Ridge. Snow frequently persisted in scattered patches on Carpenter Ridge until early or mid-April. For example, on 28 April 2010, there was still 30 cm to almost 100 cm of snow from N to S areas across the crescent shape of the ridge (Fig.1B). In 2017 approximately 15 cm of snow covered the ridge, and after that snow melted, another snowfall of 30 cm blanketed the ridge. Meadow and Summit had deeper snow and were not accessible usually until late May or mid-June or later. However, Meadow and Summit still were snow-covered on 2 June 2010 and 25 June 2017. Portions of Brokeoff Trail were not accessible until mid-June and early July in 2010 because of the much heavier snowfall.

TABLE 1. ANNUAL PRECIPITATION TOTALS IN CENTIMETERS FOR WATER YEARS (OCTOBER 1 THROUGH SEPTEMBER 30) FOR THE PRIMARY STUDY AREAS IN BUTTE COUNTY AND LASSEN VOLCANIC NATIONAL PARK (LVNP). Years are listed for when mature fruits and seeds were collected. See text for locations of weather stations, website addresses to data, and dates of access. NA = not available, NS = not surveyed.

	Snowfall (cm)		Total rainfall (cm)	
Water year	Summit	LVNP	Carpenter Ridge	LVNP
2008–2009	125	NA	119	127
2009–2010	149	253	135	147
2010–2011	208	NS	145	NS
2016–2017	254	NS	279	NS
2017–2018	119	NS	119	NS

The average daily air temperatures from the weather station near Carpenter Ridge demonstrate that Ridge was slightly cooler in the spring of 2010 than in both 2009 and 2018 (Table 2), the three years for which major phenology is presented in this paper. Average daily air temperatures for the LVNP Weather Station for 2009 and 2010 followed a similar pattern (Table 2). Air and soil temperature data taken at Ridge areas during the periods of fruit development were in the range of 15-20°C. Mid-summer air temperatures at Ridge seed and bulblet

TABLE 2. AVERAGE MONTHLY AIR TEMPERATURE IN DEGREES CELSIUS FOR SELECTED MONTHS FOR THE PRIMARY STUDY SITES IN BUTTE COUNTY AND LASSEN VOLCANIC NATIONAL PARK. Years are listed for when mature fruits and seeds were collected. See text for locations of weather stations, web site addresses, and dates of access. NS = not surveyed

Year	Month	Carpenter Ridge	Lassen Volcanic National Park
2009	April	7.7	5.4
	May	15.4	12.0
	June	16.3	13.4
2010	April	5.1	2.9
	May	8.2	5.9
	June	19.4	13.9
2011	April	5.6	NS
	May	8.2	NS
	June	14.7	NS
2018	April	8.7	NS
	May	13.9	NS
	June	19.8	NS

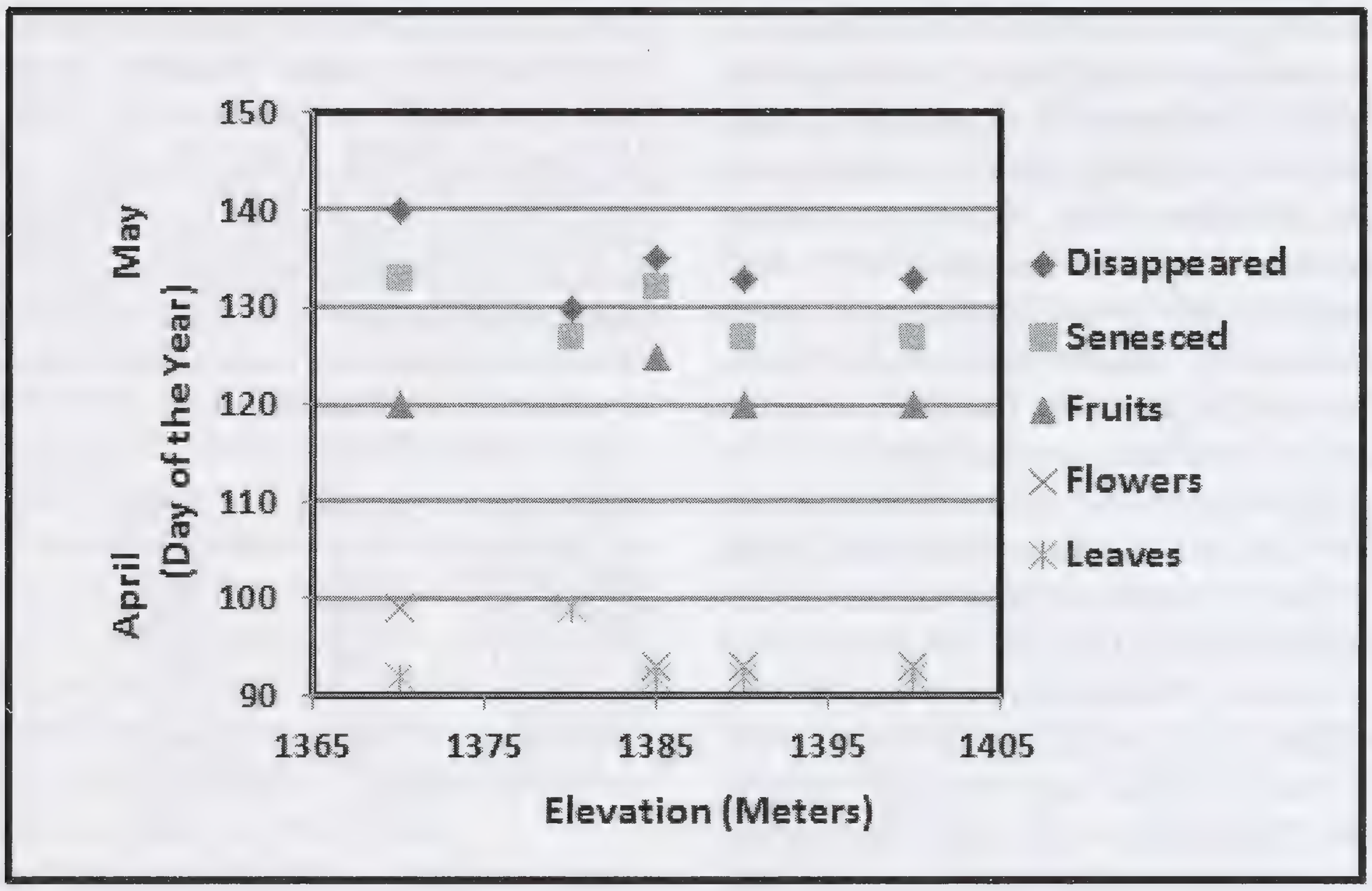

FIG. 2. Detailed phenology of *Dicentra uniflora* at the five areas of Carpenter Ridge in 2018, as representative of the typical phenology for this species. The timing of the first appearance of leaves and flowers occurred as shown by day of the year in early April 2018. Leaves and flowers appeared soon after snowmelt at the five study areas. Mature fruit development occurred in two to three weeks after first leaf and flower emergence. Senescence and disappearance of plants followed in another two to three weeks. The five columns of data points represent the phenological changes at the areas on Ridge from left to right, as follows: S, N, NE, SE and E.

planting sites were in the 30°C range; whereas mid-day soil temperatures at seed and planting sites commonly reached 40°C, or 10 degrees higher on the average, than air temperatures. These soil temperatures were almost as high as the temperature (43°C) used to dry the tubers and bulblets for evaluation of dry versus fresh weights. Mid-day air temperatures at Meadow and Summit seed and bulblet planting sites were 8 to 20 degrees less than Ridge due to the more shaded sites and were typically in the 20-23°C range. Soil temperature data taken at the Butte County sites beneath snow were in the 0.5 to 1°C range.

Plant Density

Percent cover is typically low for *Dicentra uniflora*–less than 1.5% (Jackson and Bliss 1982; Auckland et al. 2004). Cover was low at our study sites also. Number of leaves of all types from single leaves to clusters of highly dissected leaves ranged from a lowest mean of 0.025 ± SE 0.0025 per 1-m^2 at Ridge N (2009) to a highest mean of 11.325 ± SE 2.238 per 1-m^2 at Ridge S (in 2010) with single leaves being the most common. Low flower densities are also common, ranging from zero per 1-m^2 at Ridge N (2009) to 5.2 ± 1.590 per 1-m^2 at Ridge S (2010), making detection unlikely unless one visits a location soon after snowmelt and is looking specifically for this species.

Phenology

Recent. The development of *D. uniflora* from after snowmelt to senescence and disappearance usually takes six to seven weeks. Flowers change color very rapidly, usually within a week, and fruit development typically follows within another one and a half to two weeks. As the fruit develops, the flowers turn greenish and become brown, plump and firm. Fruits also become heavy and lie prostrate on the ground, and once mature, expose their seeds. Herbivory on fruits appears to occur during the maturing phase. Plant senescence typically occurs within two to three weeks after fruits mature and is noted by yellowing of the leaves, followed by browning, and shortly thereafter total withering and disappearance. Herbivory was never observed on green or yellowing leaves in this study. The typical phenological pattern is shown in Fig. 2 for Ridge areas. This general pattern may take a slightly shorter time period at higher elevations of perhaps a week (Fig. 3). The spring temperatures and snowmelt were similar in 2009 and 2018, and therefore fruits matured at about the same times in those two years in Butte County sites. Emergence of *D. uniflora* was about a month later at the locations for Ridge, Meadow, and Summit between 2009 and 2010. This pattern is similar to that observed on Brokeoff Trail in LVNP also (Fig. 4).

Historical. Herbaria collections from 1903—1998 show flowering dates from approximately 100 to 210 (as DOY) for elevations ranging from about 1200 to 3200 m (Fig. 5). As elevation increased, *Dicentra* flowered later in the year ($R^2 = 0.469$, df = 90, $P < 0.001$, $y = 76.9 + 0.04x$). In other words, for each 100 m increase in elevation, there was a 4-day delay in flowering. This trend is consistent across similar elevations used in our studies in northern California (Fig. 5).

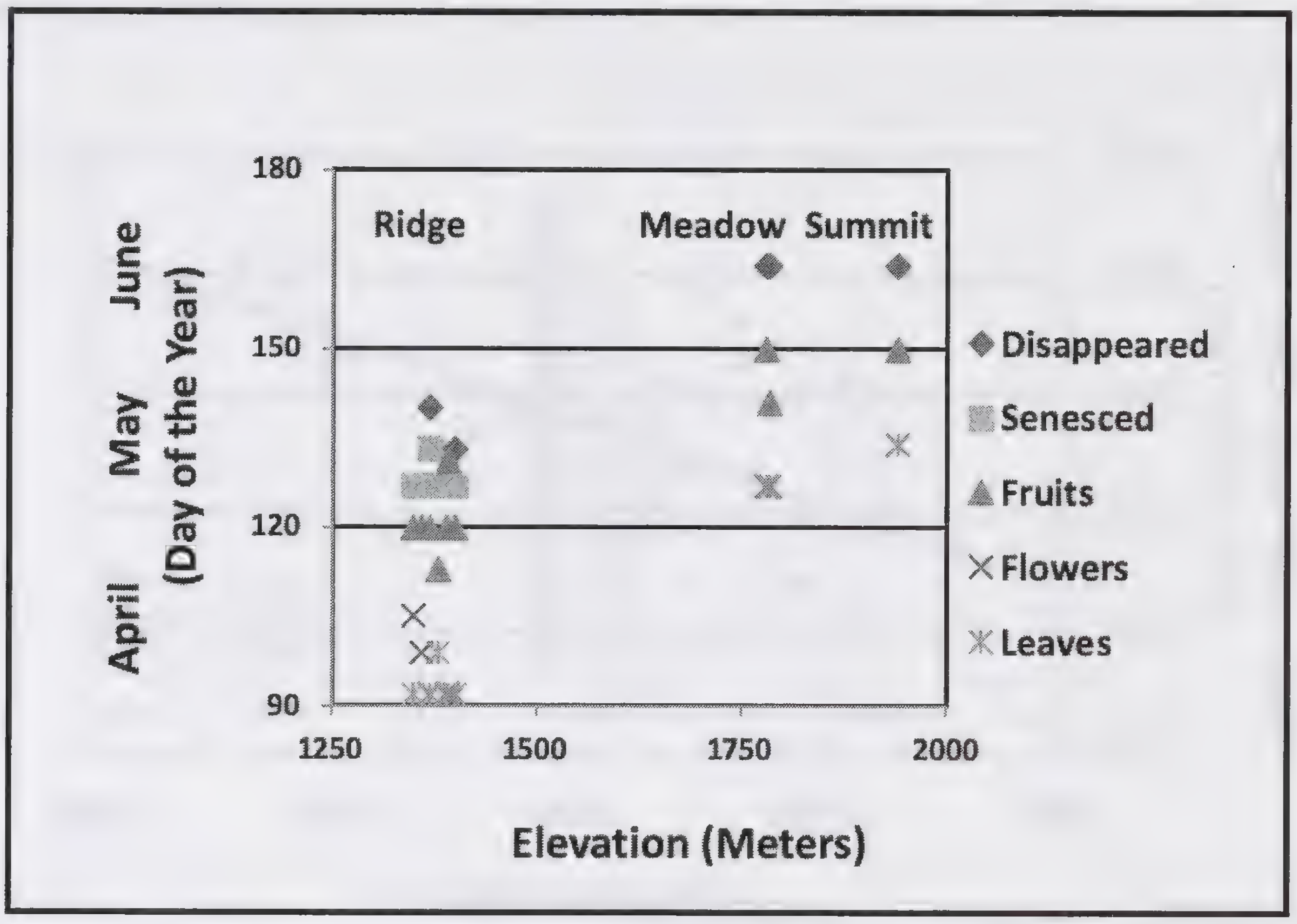

FIG. 3. Variation in phenology of *Dicentra uniflora* at the three main Butte County study sites (Ridge, Meadow, and Summit) for 2018. The timing and appearance of the first leaves and flowers soon after snowmelt is shown as day of the year. Leaves and fruits appeared in early April at Ridge (which included five study areas), and in early to mid-May at Meadow and Summit. Mature fruits appeared two to three weeks later. Senescence and disappearance of plants followed in another two to three weeks. The plants and fruits developed slightly faster at the higher elevation Meadow and Summit sites than at the lower elevation Ridge site, by perhaps one to two weeks. Symbols represent day of year for individual observations.

Reproduction and Growth

Fate of flowers in 2018. The fate of flowers on *Dicentra* plants staked in the spring of 2018 is shown in Fig. 6 and summarized across the three main sites as follows: 27-43% of the flowers produced mature fruits with seeds, 23-24% dried up, and 25-30% disappeared, often leaving the pedicels.

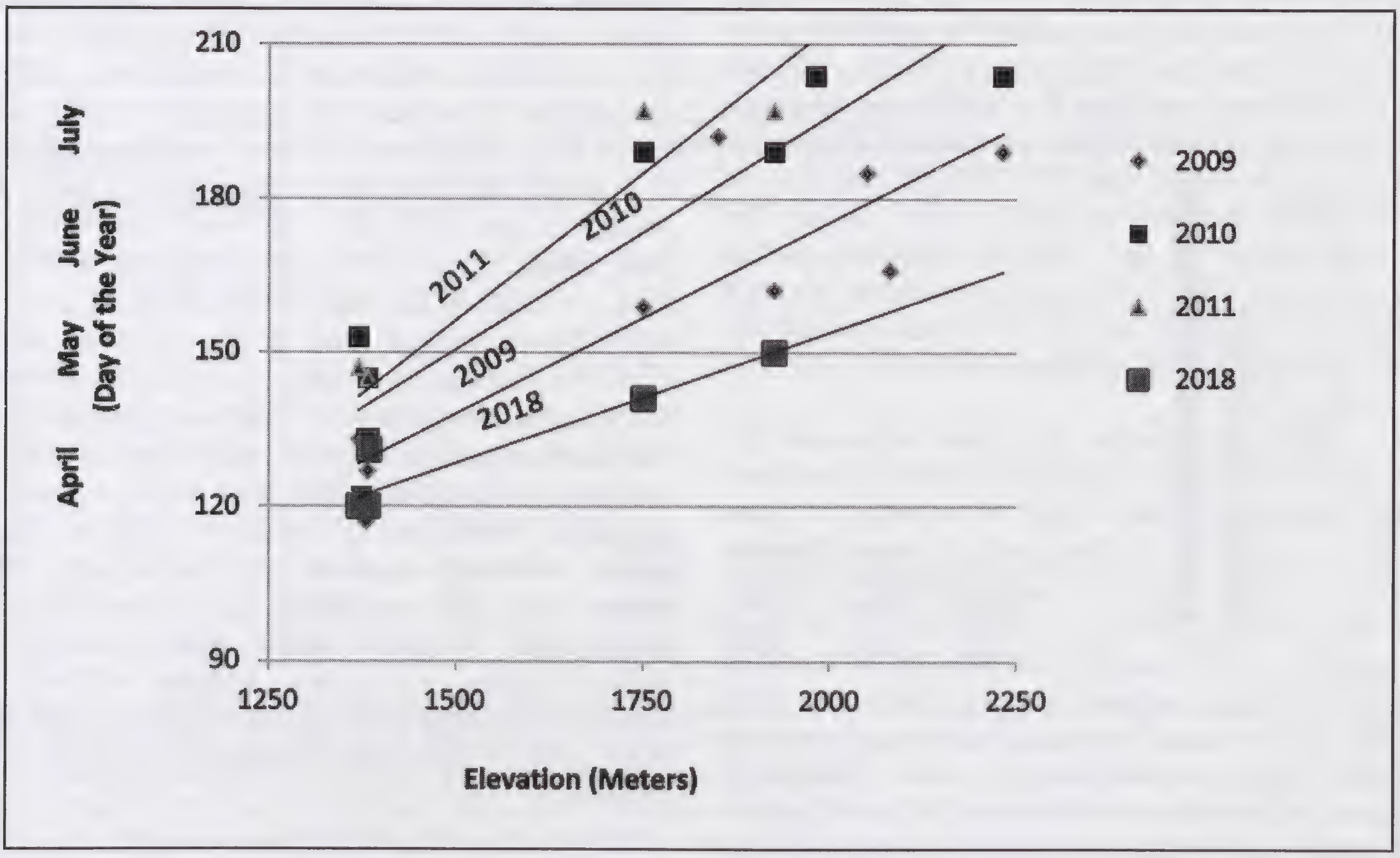

FIG. 4. Trends of mature fruit collections of *Dicentra uniflora* in 2009, 2010, 2011 and 2018 at study sites in Northern California showing influences of both elevation and weather patterns. Mature fruits were collected at Butte County and also at Lassen Volcanic National Park study sites in 2009 and 2010, but only at the Butte County sites in 2011 and 2018. The spring temperatures and snowmelt were similar in 2009 and 2018; therefore, fruits matured at about the same times in the Butte County sites in those two years. There was a cooler spring and later snowmelt in both 2010 and 2011 than in both 2009 and 2018; thus, fruits of *D. uniflora* matured later in 2009 and 2018.

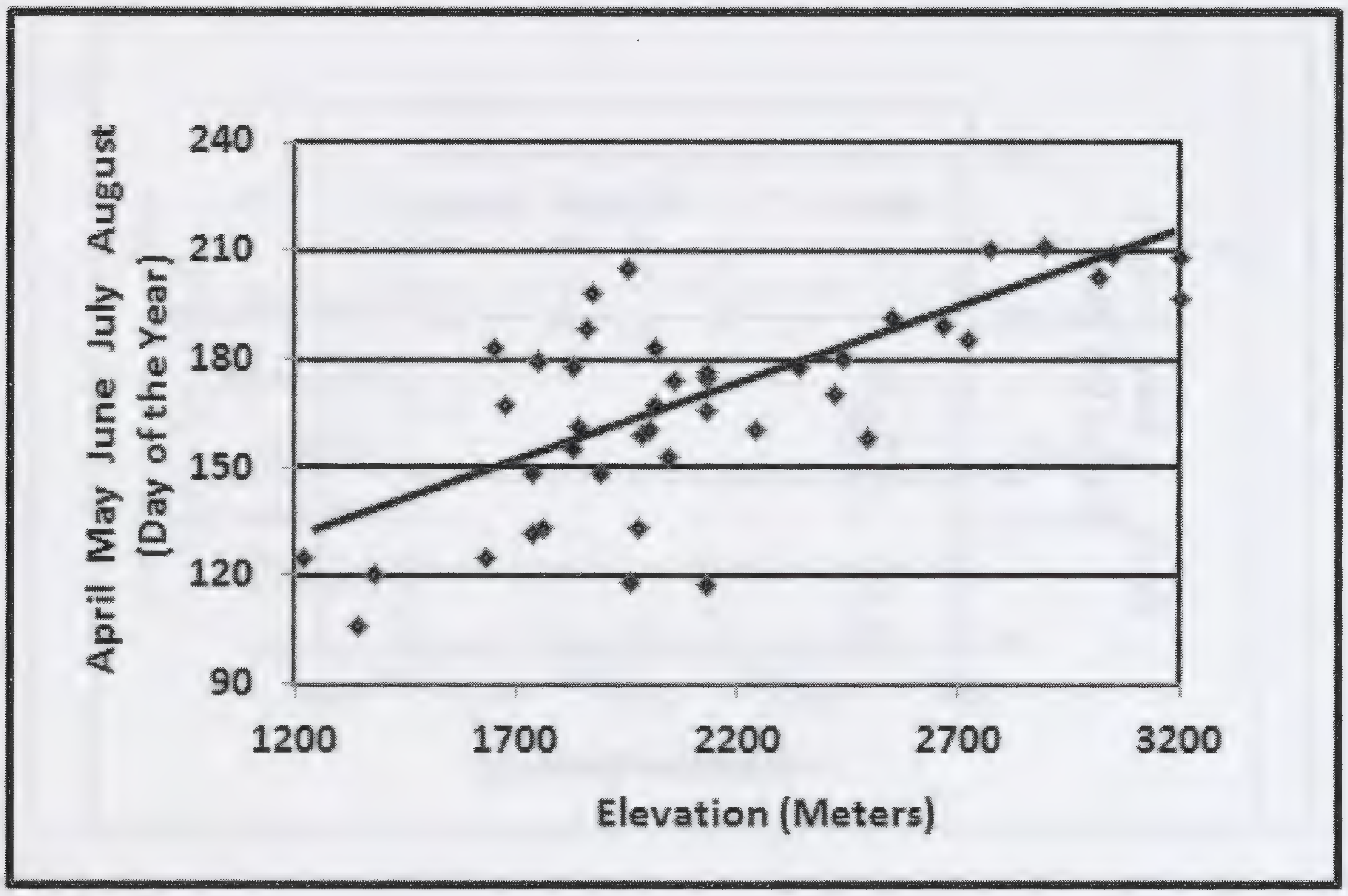

FIG. 5. Historical phenology of *Dicentra uniflora* in Northern California as indicated by collections of flowering herbarium specimens from 1903 through 1998. This linear regression shows the approximate day of the year of collection versus elevation from April through early August for 1903-1998. These collections were from 1250—3200 m in elevation, with higher elevation collections into early August.

Seeds per fruit. The number of mature seeds per fruit at the three main Butte County study sites varied somewhat in the four years that larger samples (n = 13 - 32) were obtained (Fig. 7A). These results show that the two higher elevation sites (Summit and Meadow) averaged more seeds per fruit than the lowest site, Ridge (ANOVA, F = 17.34, P <0.0001, df = 4). For example, on average Summit had more seeds per fruit than the three areas at Ridge, NE, SE and S (Tukey Post-hoc Test, P <0.009) and Meadow had more seeds per fruit than two areas at Ridge, SE and S (Tukey Post-hoc Test, P = 0.0028). Seeds from fruits listed for Ridge S in 2018 in Fig. 7A are the same fruits listed in the fate of recovered staked flowers shown in Fig. 6. The average number of seeds per fruit in *D. uniflora* in the 227 fruits counted for the four years at the three sites listed in Fig.7A was 62.8 ± SE 3.35.

Four additional samples at higher elevations (at the secondary study sites) had the following numbers of seeds per fruit (mean ± SE): Humboldt, 15 June 2009, 80 ± 6.6 (n = 32); Brokeoff, 30 June 2009, 64 ± 3.6 (n = 32); Brokeoff, 8 July 2009, 61 ± 4.2. (n = 22), and 23 July 2010, 67 ± 4.1(n = 25). Average seeds per fruit of *D. uniflora* for this entire study in the southernmost Cascade Range, combining data from the three main sites and the two secondary study sites listed here was 65.6 ± 2.6 (n = 325 fruits), in contrast to a mature seed count of 58 (n = 1) given by Courtney and Scotter (2018) and a reported seed count "greater than 50" per fruit (n = 82) by Rayl (2002).

Percent seed set. At all sites, counts of ovules that did not mature permitted determination of percent seed set. The mean number of ovules (developed and undeveloped) found in mature fruits listed for the three main study sites (Fig. 7B) was 70.4 ± SE 3.3. These ovules in mature fruits ranged from minute (possibly unpollinated) to partially developed, but wrinkled, and/or white–in sharp contrast with the black mature seeds. High percent seed set, ranging from 81–95%, occurred in the main sites of this study (grand mean of 87.6% in Fig. 7B), but with the two-way ANOVA indicating a significant difference among the three main locations (F = 11.41, df = 4, P <0.001). High percent seed set also occurred in Humboldt and Brokeoff sites (mean ± SE): Humboldt, 15 June 2009, 82 ± 3.7 (n = 19); Brokeoff 30 June 2009, 92 ± 2.1 (n = 32); Brokeoff, 8 July 2009, 84.5, ± 3.5 (n = 22) and 23 July 2010, 87.8 ± 1.9 (n =25). Mean percent seed set for all study sites was 87.4. No damage to ovules or seeds was observed in the 325 fruits examined to determine percent seed set, although occasional thrips were seen in the fruits, and occasional aphids were seen on the outside walls of fruits. Herbivory of seeds or fruits is described below. Although seed set per fruit is high, 80% or higher (Fig. 7B), we believe this occurs due to self-pollination. We have never observed any flower visitors during our many seasons of field visits. Stamens are appressed to the stigmas in the flower. Rayl (2002) had seed production in her bagged flowers.

Mature Seeds and Elaiosomes

Two hundred fifty shiny, black mature seeds from Ridge, weighed immediately after removing from fruits in May 2009, had an average weight per seed bearing an elaiosome of 0.5488 ± SE 0.0139 mg (Fig.

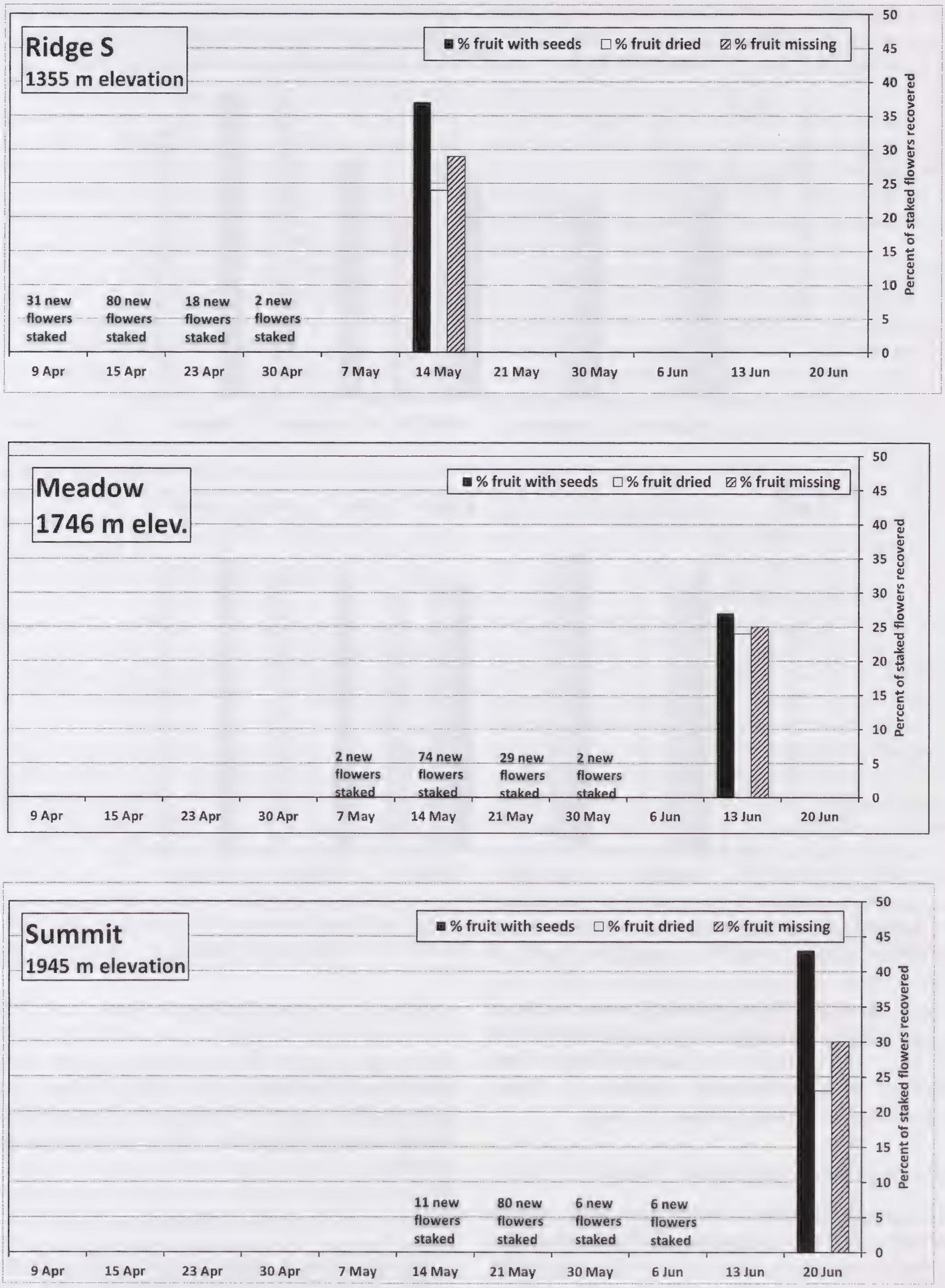

FIG. 6. Fate of staked *Dicentra* flowers at the three main study sites in Butte County in 2018. Each panel represents results at one of the three sites, showing dates flowers were staked (over a four-week period at each site) and dates when the fruits were recovered and assessed at each site. The three panels all have the same dates in 2018 listed across the horizontal axis to show how plants at the lower-elevation site (Ridge S—top panel) flowered and fruited earlier than at the other two, higher-elevation sites (Meadow and Summit). Fruits recovered at time of fruit maturation and plant senescence, were scored as percent of total flowers marked; percentages do not total 100% at a site because some stakes could not be relocated. Percent fruits with seeds = mature seeds present; % fruit dried = remains of ovary or young fruit present, but not producing seeds; % fruit missing = fruit gone, with or without pedicel still present.

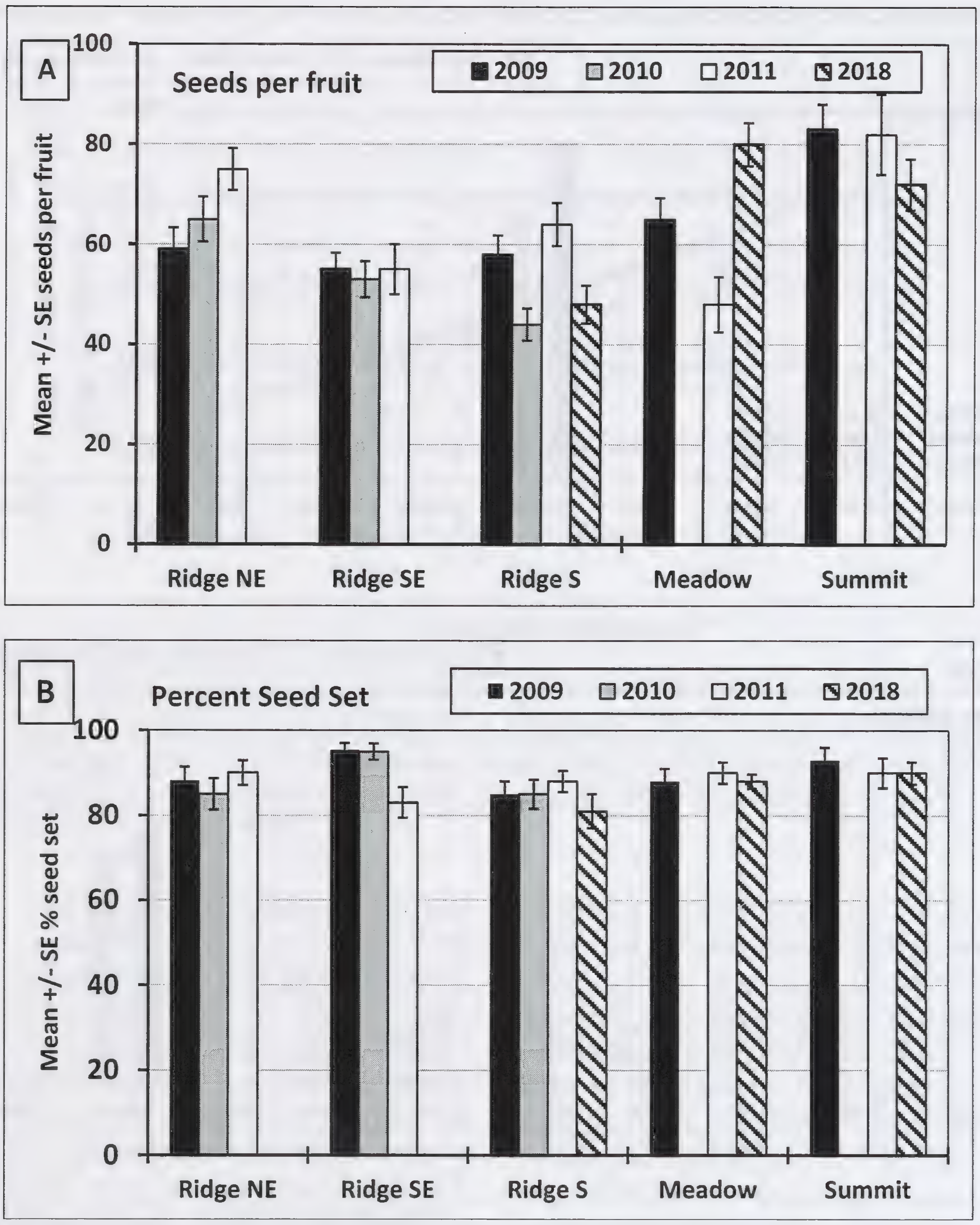

FIG. 7. Reproductive success in *Dicentra unilfora* at five study areas, over four years (n = 13 at Meadow, 2011; n = 18 - 32 in other years and areas). A. Mean ± SE seeds per fruit. B. Mean ± SE % seed set (n same as in Fig. 7A).

1C). Two hundred fifty additional seeds without elaiosomes had an average weight of 0.4994 ± SE 0.0178 mg. Thus, fresh elaiosome weight was estimated to be approximately 0.0494 mg. Elaiosomes detached very readily from the seeds.

Herbivory on Reproductive and Vegetative Parts

Each year, at all Butte County study sites, tracks of mule deer, *Odocoileus hemionus* Rafinesque, or the deer themselves were seen, but were not seen specifically browsing on *Dicentra* plants. Tunneling by Botta's pocket gopher, *Thomomys bottae* (Eydoux and Gervais), was common in the Meadow and Summit (but not Ridge) sites, but no specific destruction of *Dicentra* plants was noted. Bulblets of *D. uniflora* might be dispersed in the soil during tunneling by gophers, resulting in asexual reproduction (e.g., at Meadow and at Summit). A few examples of ants in fruits, or even carrying *Dicentra* seeds, have been recorded (at Summit, 16 July 2011 and 6 July 2018), but the ants were not collected or identified to species. At Summit, on 8 June 2018, a 16 mm-long black caterpillar or larva (Fig. 1G) was found on a partially eaten fruit. Also, an adult butterfly of *Parnassius clodius* (Fig. 1H) was captured nearby. Both were identified by Don Miller, California State University, Chico (personal communication).

Seed Plantings

Heavy erosion impacted the bulk plantings of seeds in the winters of 2009-10 and 2010-11. Remaining strips of paper bearing seeds and seedlings in soil were extracted with care, but seedlings were very small and delicate (Fig.1D), and some may have been missed during examination of the strips with dissecting microscopes. Plantings of individual seeds provided additional observations of the early germination features of *D. uniflora*.

Germination of at least some of the bulk-planted seeds occurred during the winter under snow. At Ridge N two strips of seeds planted on 15 July 2009 were dug on 17 December 2009. Black, hard seeds were found, with no signs of germination. But the next year, winter germination was confirmed with seeds planted in 2010, when strips bearing two and five germinated seeds were found at Ridge N on 4 February 2011. Cotyledons of seedlings appeared aboveground in all five different study areas at Ridge in April and May of 2010 and 2011. Each seedling had a single un-lobed cotyledon (Fig. 1D), sometimes with the seed coat still attached at the tip. Seedlings appeared later in the year at the higher elevation sites, visible at the soil surface soon after the snow melted, on 8 July 2010, with 29 cotyledons per paper strip at Meadow and 11 at Summit.

Many seedlings, apparently after photosynthesizing for a just few days (or possibly longer under the snow) had produced a bulblet (Fig. 1D). The largest sample of intact seedlings, collected when they were just reaching the soil surface (Ridge E and Ridge SE combined, on 12 May 2011, n = 36), had the following features (mean ± SE): length from tip of cotyledon to tip of root, 32.4 ± 1.83 mm (range 11-55 mm); maximum diameter of bulblet (n = 4) 1.0 ± 0.11 mm (range 0.7-1.2 mm).

A sample of seedlings about 3 weeks older that year (on 2 June 2010 at Ridge N) were somewhat larger: length from tip of cotyledon to tip of root (n = 8), 34.8 ± 1.9 mm (range 29.7-43.7 mm); maximum diameter of bulblets (n = 7) 1.43 ± 0.1 mm. Cotyledon blade (n =13) width was 1.9 ± 0.1 mm and length was 4.2 ± 0.2 mm. Measurements of seedlings from individual seed plantings in grid patterns compared well with the measurements presented here from bulk seed plantings. Seedlings at the three main sites (at different elevations) dried up above ground a few weeks after emergence, at which time the leaves of the adult plants were also becoming yellow or brown at senescence.

Below Ground Parts

Tubers. Representative below ground parts of a *Dicentra uniflora* plant are shown in Fig. 1F. Two new, pale tubers produced by the end of the spring growing season are shown in front of parts of two dark, withered tubers from the previous year that had produced the leaves and flowers in 2010. Fig. 1F also shows that fine roots had emerged from among the bulblets on the stem axis near the tops of tubers by early November. Average number of new tubers per plant was 1.6 ± 0.2 (n= 26). The depth to the tops of tubers on plants occurring in clusters ranged from 3.2 to 10.7 cm in the rocky, loamy or sandy-loamy soils of the sites.

Fresh weights (mean ± SE in g) were determined for new tubers collected at Ridge at two times in 2010. On 12 June fresh weights (0.366 ± 0.035, n =25) were higher than fresh weights (0.161 ± 0.027, n = 26) collected on 4 November. The June sample consisted of plants dug at the end of the photosynthesizing/flowering season. The November sample comprised plants that had persisted through the hot, dry summer season in the soil, but had received 20 mm rain by 8 September and 204 mm total rainfall just before being sampled.

Dry weights of the tubers collected on 12 June (0.188 ± 0.018) were significantly higher (Student's t-test, t = 2.54; $P < 0.05$) than the dry weights of tubers collected on 12 November (0.118 ± 0.017). Grams dry weight lost over the summer were 36.98% of the dry weight of the June plants.

The mean maximum diameter (in mm) of new tubers, did not differ between the two samples (Student's t-test, t = -0.748, P = 0.458; June, 5.8 ± 0.2 versus November, 5.4 ± 0.25). Average length of tubers on flowering plants was 21.0 ± SE 2.5 mm. Average number of tubers per plant was 1.6 ± 0.2, determined from the November sample.

Bulblets. Plants collected on 4 November 2010 had (mean ± SE) 8.7 ± 1.0 whitish, ellipsoidal bulblets per plant clustered on the condensed stem axis to which tubers were also attached (Fig. 1F). Mean trait values of the bulblets (n = 31) were: length 4.0 ± 1.2 mm, maximum diameter 1.8 ± 0.1+ mm, fresh weight of 7.0 ± 0.3 mg, and dry weight of 6.6 ± 0.3 mg. It is not known if bulblet size (e.g., a range in length of 2.6 mm to 5.6 mm) relates to an increase in succeeding years, or if bulblets of different sizes on a plant were all produced in the same year and grew to different sizes. Bulblets were white and mealy throughout, with no obvious sign of an embryonic plantlet under a dissecting scope, although a very minute apparent bud meristem was visible at the base of the bulblet, similar to that reported by Walton and Hufford (1994) for *D. cucullaria.* All flowering *D. uniflora* plants sampled had bulblets, and most seedlings produced a single bulblet at the base of the petiole of the cotyledon (Fig. 1D). Bulblets planted in 2009 and 2010 produced small plants, each with a whitish (new) bulblet, and discolored remains of the old bulblet, and a small tuber.

DISCUSSION

Phenology

Our studies provide the first detailed quantitative information on the emergence of leaves and flowers of *D. uniflora*. The ephemeral nature of *D. uniflora* and the variation in weather phenomena from year to year require multiple years to understand the life history of this species. For example, in early June 2017, approximately 15 cm of snow-covered Ridge and numerous *D. uniflora* flowers emerged shortly after snowmelt and were marked with wooden stakes. Within a week, another snowfall of 30 cm blanketed the site, and nearly every marked flower and many new emergent leaves were frozen and lost for 2017. Meadow and Summit were visited in late June 2017, and numerous flowers were marked at both locations. Over the next two weeks these sites were visited and nearly all flowers/fruits were missing, probably due to herbivory. Thus, 2017, which started as an apparently "good flower and fruit spring," was essentially lost as a study year, with little phenological data collected at any site. The spring of 2018, by contrast, was a very good year for growth and seed production in *D. uniflora*, and we were able to collect excellent data at all three main study sites in northern Butte County.

Previous authors have noted the emergence of *D. uniflora* soon after snowmelt in northern California and the mountains of the western United States and Canada (Stern 1961; Hickman 1976; Jackson and Bliss 1982; Jackson 1985; Rayl 2002; Auckland et al. 2004; Courtney and Scotter, 2018), but there is no information on the time required from first appearance until fruiting and senescence. There is general information available on earlier emergence and flowering at lower elevations near 1200 m in British Columbia (Courtney and Scotter 2018) or high as 3280 m in the Slate Creek Valley in the Sierra Nevada of California (Jackson and Bliss 1982). In California herbarium collections, a flowering date as early as 28 March 1988 at 1209 m and as late as 11 July 1911 at 2895 m have been recorded. The range of elevations for the primary sites of this study, from a low of 1370 m for Ridge to 1945 m for Summit, thus fall in the mid-range of elevations for this species. Higher elevations from 2000 to 2600 m are included in two of the earlier years of our study (2009, 2010); thus, findings from this study have general applications to this species throughout its geographic range. The range of elevations from 1370 m (Ridge) to 1945 m (Summit) provide a four to seven-week period of snowmelt from the lower elevation to higher elevation; thus, as lower populations were maturing to fruit development, higher populations were just beginning to emerge. In 2018, it was even possible to mark the edge of the snowfield at Meadow and Summit study sites and record the emergence of flowers as the snowline receded. Figs. 3 and 4 illustrate the phenological patterns observed with snowmelt in our region in northern California for four years. Similar patterns of phenology are to be expected through the years throughout the range of *D. uniflora*.

Herbarium collections have focused on the flowering dates of this plant and its unique appearance. Leaves can resemble other plants and without the flowers, it can be easily overlooked (Courtney and Scotter 2018). The flowers mature to fruit rapidly in only two to three weeks, turning from green to brown. They tend to be prostrate on the ground (Berg 1969) as they become mature, begin dehiscing, and shrinking, making them even more difficult to observe. Given the low density of the flowers, marking flowers with small numbered wooden bamboo stakes was essential for tracking flowers and fruits and evaluating their fate (Fig. 6).

Seeds, Germination, and Seedlings

Nature of seeds and their elaiosomes. Growth and maturation of *Dicentra uniflora* seeds were described by Berg (1969). He illustrated that the elaiosome was of epidermal origin on the developing ovule, and that at seed maturity an elaiosome consists of only between six and eleven giant cells that "contain great quantities of fatty oils" (as determined by tests using Sudan IV). Berg noted that an elaiosome breaks loose from a seed very easily, and that this may be why Stern (1961) described *D. uniflora* seeds as lacking elaiosomes in his systematic treatment of the genus. Fukuhara (1999) presented an electron microscope view of a *D. uniflora* seed bearing an elaiosome and noted that in this species the elaiosome is globose or irregularly elongated, "reaching 0.5 to 2.5 times as long as the seed." Elaiosomes are shown on the seeds in Fig. 1C.

Berg (1969) considered this species to be myrmecochorous and speculated that the "lustrous black" seed coat, as well as the elaiosome, were both attractive to ants. Berg illustrated a fruit apparently chewed open by ants, and described two small field experiments from 1964 where *D. uniflora* seeds set out in "depots" (small piles of 10 fresh seeds) were carried away in a few minutes by ants (*Formica lasioides* in El Dorado County, and *F. fusca* in Alpine County, CA). In the field, we have only very rarely observed ants taking elaiosomes from *D. uniflora* fruits, but suspect that ant dispersal is at least an occasional part of the life history of this species in Butte County. Berg (1969) discussed in detail the probable evolution of myrmechochory in *Dicentra.* He suggested that *D. uniflora*, showing a "minimum number of diaspores produced at ground level" probably represents a unique pathway ("blind end") in evolution of ant dispersal in the genus, as compared with taller myrmechohorous species like *D. formosa*.

Seed germination. Stern (1961) noted that seeds of *Dicentra* need three months of stratification before germination; he may have been referring to *D. formosa* and not *D. uniflora.* No earlier information is available on the germination of *D. uniflora* seeds. Some of the features we describe are similar to those described for other geophytes: germination in the soil during the winter, fast production of underground parts that remain dormant over the summer, and a short life above ground before dying down to a dormant below ground organ (Dafni et al. 1981). These life cycle features are known to occur in several other geophytic species that occur with *D. uniflora* at all three main study sites, such as *Triteleia ixioides* (W. T. Aiton) Greene subsp. *anilina* (Greene) L. W. Lenz, (Kannely and Schlising 2014), *Allium campanulatum*, and *Sanicula tuberosa* (Schlising, unpublished data).

It is particularly noteworthy that the tiny *Dicentra* seedlings have the only several weeks to establish a below ground organ that will initiate growth the next year, formed by photosynthesis (and possibly by transferring nutrients from the endosperm in the seeds) and growing a structure above the root that has been called a "bulblet" by Stern (1961), or referred to as a "bulbous leaf base" by Walton and Hufford (1994). These small white structures (Fig. 1D) on the seedlings are only about 10% of the size of bulblets that are found on on mature (flowering) individuals (Fig. 1F).

Finding an apparently single cotyledon in this dicot was surprising (Fig. 1D). However, the phenomenon of "pseudomoncotyly" (or "monocotyledony") in the dicots is briefly described in older textbooks of plant morphology (e. g., Eames 1961) and is reprised more recently based on experimental studies of embryo morphogenesis (Titova 2000). However, mention of the single cotyledon specifically for *Dicentra* is very rare in the literature, [e.g., "1 in tuberous *Corydalis* and a few *Dicentra* species" (Lidén 1993)].

Herbivory on Whole Plants or Reproductive Parts

It is likely that the "missing" fruits described under "Fate of Flowers in 2018" relates in part to having been grazed by black-tailed deer. Percentages of developing fruits probably lost to deer may be high: Ridge S: 29%; Meadow: 25%; and Summit: 30% in 2018 (Fig. 6), and in all years of this study missing fruits—often with the pedicel still present—were noted at each main study site. Rayl (2002) reported that rodents ate a few of the non-bagged flowers/fruits in her study but provided no information on which species of rodents. She also reported 18% (in 2000) and 16 % (in 2001) of her non-bagged flowers/fruits were lost to predation. These percentages are slightly smaller than those seen in our study in 2018 (Fig. 6). Cameras in the field would help ascertain loss to deer. Rick Whittsell (Chico State University, personal communication), who has studied the black-tailed deer in Butte County, confirms that they are able to select small parts of plants with their tongues. Thus, in the early spring (when *Dicentra* fruits are forming) they could be a nutritious food source when there are still few sources of fresh plant growth available. Is it also possible, that *D. uniflora* has achieved some of its wide geographic range via dispersal of seeds in feces of deer. Myers et al. (2004) reported that seeds from 70 plant species, including native herbs, were germinated from fecal pellets of white-tailed deer (*Odocoileus virginianus* Zimm.) in New York State. They concluded that white-tailed deer represented a significant and previously unappreciated vector of seed dispersal. One unknown aspect concerning herbivory is whether the alkaloids common in species of *Dicentra* are toxic to deer, as this species has been reported to cause occasional livestock poisoning in cattle (Stern 1961).

The mature fruits that we collected for seed counts were not totally desiccated and dry, and Berg (1969) even considered fruits to be "greenish and somewhat fleshy at maturity, and made of living chlorenchyma and not desiccated tissues." Thus, the discovery of the caterpillar of *Parnassius clodius* on an apparently masticated fruit (still attached to the plant but lying on the ground) suggests that this species could potentially be responsible for some destruction. Scott (1986), Pyle (2002), and James and Nunnallee (2011) describe the butterfly as having *D. uniflora, D. pauciflora* and *D. formosa* as host plants on which the larvae feed in spite of poisonous alkaloids in the plant tissues (Scott 1986). All three species of *Dicentra* occur at Meadow and Summit study sites. Adult butterflies lay over-wintering eggs, often in the litter on the ground in the vicinity of *Dicentra* plants (Pyle 2002; James and Nunnallee 2011). The several instars of the larvae apparently consume *Dicentra* leaves and possibly green fruit tissue during the short, several-week above ground growth period of the plant. Furthermore, the larvae feed nocturnally (Pyle 2002). This may explain why we did not observe any larva earlier in the study, although we have not noted insect damage on the leaves either. The larva collected was a late instar of *P. clodius* (Fig. 1G).

Leaf Base Tubers (Bulblets)

Function of the leaf base tubers (bulblets) produced on flowering *D. uniflora* plants, as well as on its seedlings, can be partially understood based on the work of Walton and Hufford (1994). These authors published detailed work on the below ground structures in the closely related *D. cucullaria*, which flowers early in the spring in deciduous forests in the northeastern U.S. and adjacent Canada; they included brief comments on *D. uniflora*. The underground bulblets of *D. uniflora*, like those that we have measured and have also planted, are presently referred to as bulblets in several floras (e.g., Stern 1961; Baldwin et al. 2012), and we have used that term in this study. Bulblets in *Dicentra* are leaf base tubers, each with the potential for producing a new plant from a minute, undeveloped bud at its base, if the leaf base tuber is detached from the parent plant as stated by Walton and Hufford (1994). Walton and Hufford (1994) noted that these bulbous leaf bases in the four related species of *Dicentra* (*D. cucullaria, D. canadensis* Walp., *D. pauciflora*, and *D. uniflora*) are unique in the angiosperms.

Walton and Hufford (1994) also suggested that stored carbohydrates in "amyloplast-filled storage parenchyma cells" in these leaf base tubers (bulblets) of *D. cucullaria* may be utilized in forming aboveground organs by this plant during its short growing season. Photosynthesis occurring at that time provisions new leaf base tubers (bulblets). Walton and Hufford (1994) describe continued belowground development during the summer months for *D. cucullaria*.

However, unlike *D. cucullaria*, *D. uniflora* has a large, fleshy root-like tuber, in addition to bulblets. The shrinking of the old tuber in *D. uniflora* probably provides carbohydrates to the emerging flowering plant, and the production of a new tuber is, at least in part, provisioned by photosynthesis. Once *D. uniflora* plants senesce, no further growth would be expected in the belowground tubers and bulblets during the dry, hot summer months in Butte County.

The production of a bulblet by a *D. uniflora* seedling (Fig.1D)—very quickly before summer drought sets in—is the only way a seedling can survive to a second year. Usually a *D. uniflora* plant in its second spring bears a brownish, shrunken (depleted) bulblet, a new whitish bulblet, and also a small tuber (Fig. 1E). Harper (1977) pointed out that it is not unusual for geophytes to have a long juvenile phase and require four to seven years or longer to reach flowering age. It is not known how many years it takes before an individual flower is produced in *D. uniflora* (Mackey, unpublished data).

Potential Historical Change in Phenology

The study areas at Carpenter Ridge are at the lower elevation of *D. uniflora* in Butte County. Areas here are aligned along a Crescent (Fig. 1A) with exposure from southwest to north, with area N warmer and area S colder than the other areas evaluated at this site. Therefore, snowmelt is earlier at N than at S. Meadow and Summit are at intermediate elevations over the range of elevations of *D. uniflora* in California. Analysis of trends in snowpack across California have indicated reduced snowpack at intermediate and lower elevations in more recent years (Howat and Tulaczyk 2005; He et al. 2015). There is also an apparent increase of slightly less than one degree C from 1970 to 2017 in statewide annual average temperatures, and a shift of almost a month earlier in average peak runoff in the Sacramento River system from mid-April to mid-March (OEHHA 2018). A better understanding of the life history responses and growth of *D. uniflora* to snow cover, snowmelt, and dry and wet seasons could potentially provide information on the long-term climate change in northern California.

Our ongoing use of field plantings of seeds and bulblets and our continued long-term evaluation of flowering and underground features will provide a better understanding of the timing and growth patterns of this ephemeral geophyte.

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APPENDIX 1

Voucher specimens for *Dicentra uniflora* are filed at California State University, Chico (CHSC). Butte County, CA, close to Tehama County line, on Carpenter Ridge, southwest of Butte Meadows, 2 mi E of junction with Highway 70 (T25N, R3E, NW ¼ of NW ¼ Section 1), elevation 4350 feet; volcanic mudflow outcrop within conifer forest; 27 April 2009; *R. A. Schlising 4471 and H. E. Mackey, Jr.* Butte County, CA, close to Tehama County line, on Carpenter Ridge, southwest of Butte Meadows, 2 mi E of junction with Highway 70 (T25N, R3E, NW ¼ of NW ¼ Section 1), elevation 4350 feet; volcanic mudflow outcrop within conifer forest; 13 May 2009; *R. A. Schlising 4472 and H. E. Mackey, Jr.* Butte County, CA, E of Jonesville, near NE tip of the county, ca. 0.75 mi S of Humbug Summit, on Humbug Summit Road; margin of forest of *Abies magnifica*; in conifer litter; 28 June 2017; *R. A. Schlising 4678 and H. E. Mackey, Jr.* Butte County, CA, 6.6 km east of Jonesville, and 0.32 km south of the road leading up Scotts John Creek, on U.S. Forest Service road 26N27, at 40°06′21.0″ latitude N, 121°25′35.40″ longitude W, and at 1746 m elevation; in open, drying meadow between dense forest of mainly *Abies concolor* and meadow remaining wet all summer; 6 June 2018; *R. A. Schlising 4679 and H. E. Mackey, Jr.*

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TREE MORTALITY IN BLUE OAK WOODLAND DURING EXTREME DROUGHT IN SEQUOIA NATIONAL PARK, CALIFORNIA

ADRIAN J. DAS, NICHOLAS J. AMPERSEE, ANNE H. PFAFF, NATHAN L. STEPHENSON
U.S. Geological Survey, Western Ecological Research Center,
Sequoia and Kings Canyon Field Station, Three Rivers, CA 93271
adas@usgs.gov

TEDMOND J. SWIECKI AND ELIZABETH A. BERNHARDT
Phytosphere Research, Vacaville, CA 95687

PATRICIA K. HAGGERTY
U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center,
Corvallis, OR 97330

KOREN R. NYDICK
Sequoia and Kings Canyon National Parks, Three Rivers, CA 93271
Currently: Rocky Mountain National Park, Estes Park, CO 80517

ABSTRACT

Blue oak woodlands in California have been a focus of conservation concern for many years. Numerous studies have found that existing seedling and sapling numbers are inadequate to sustain current populations, and recent work has suggested that blue oak woodlands might be particularly vulnerable to a warming climate. California has recently experienced a drought of historically unprecedented severity, resulting in the mortality of tens of millions of trees, including an apparent spike in mortality in oak communities. Here we present the results of a survey of tree mortality and composition in blue oak woodlands in Sequoia National Park. We found that 18% (95% CI = 14–24,) of all standing trees and 23% (95% CI = 17–30) of standing *Quercus douglasii* Hook. & Arn. (blue oak) were dead, substantially higher than proportions of dead trees recorded in pre-drought datasets, which showed 4% (95% CI = 2–9) standing dead for all trees and 5% (95% CI = 4–7) dead or 8% (95% CI = 4–16) standing dead for blue oak. Furthermore, much of this mortality appeared to be recent. Based on foliage or fine twig retention, 19% (95% CI = 14–26) of blue oak and 23% (95% CI = 16–31) of *Quercus wislizeni* A. DC. (interior live oak) appear to have died recently. In contrast, only 5% (95% CI = 3–8) of *Aesculus californica* (Spach) Nutt. (California buckeye) and 5% (95% CI = 2–11) of *Fraxinus dipetala* Hook. & Arn. (California ash) appear to have died recently. Even after such high mortality, with blue oak basal area dropping by 26% (from 9.5 m^2/ha [95% CI = 7.4–11.6] to 7.0 m^2/ha [95% CI = 5.3–8.7]), blue oak remains the dominant species in these ecosystems. However, given the lack of recruitment and the apparent vulnerability to extreme drought, blue oak populations may be at risk for severe decline if such mortality events become more frequent.

Key Words: blue oak, drought, *Quercus douglasii*, tree mortality, Sequoia National Park.

Oak woodlands are an iconic part of the California landscape and have been a focus of conservation concern for many years (Waddell and Barrett 2005). In fact, hardwood forests in general comprise an estimated 40% of forested area in California and provide many benefits to the state, including grazing, forest products, biodiversity, and recreational opportunities. Blue oak woodland, which forms a peripheral ring around California's Central Valley, is the most common hardwood forest type, covering an estimated 1.23 million hectares (Waddell and Barrett 2005).

Numerous studies have noted an apparent lack of recruitment in blue oak woodlands, with seedling and sapling numbers seemingly inadequate to sustain existing populations (Bolsinger 1988; Swiecki et al. 1997; Waddell and Barrett 2005). Tree ring studies have supported this contention, finding little recruitment after an apparent regeneration peak in the mid-1800's and early 1900's (White 1966; McClaran and Bartolome 1989; Mensing 1992; Gervais 2006; Stahle et al. 2013). Although interpretation of the regeneration peak itself is somewhat complicated by a tendency for blue oak to resprout and by its variable and very slow height growth, there seems to be general agreement on the lack of adequate recruitment, at least in some areas, since that time (Mensing 1992; Swiecki and Bernhardt 1998; Koenig and Knops 2007; Stahle et al. 2013). Various explanations for this regeneration gap have been investigated, including fire suppression, competition from non-native annual grasses, grazing, and land use changes (McClaran 1986a, b; Gordon et al. 1989; Allen-Diaz and Bartolome 1992; Mensing 1992; Swiecki et al. 1993; Gordon and Rice 2000; Swiecki and Bernhardt 2002).

More recently, there has been heightened concern that blue oak might be at particular risk in a warming climate. Research suggests that suitable habitat for blue oak might shrink by over 50% by the end of the century, while also shifting northward (Kueppers et al. 2005). As with all forests, oak woodlands are likely to be vulnerable to the increasingly severe and potentially more frequent droughts that accompany warming temperatures (Brown et al. 2018). For example, reports indicate that the recent California drought (2012 through 2016) resulted in the mortality of over 100 million trees, including high levels of mortality in oak woodlands (Moore et al. 2017, 2018). The drought was the most extreme in the ~120-year instrumental record, partly as a consequence of the associated higher temperatures (AghaKouchak et al. 2014; Griffin and Anchukaitis 2014; Williams et al. 2015).

With recruitment lacking and the mature tree population suffering heightened mortality, the blue oak woodlands ecosystem merits particular attention. Yet, while there have been extensive examinations of recruitment and periodic surveys of blue oak woodland extent and overall changes in growing-stock volume (e.g., Waddell and Barrett 2005), there have been very few examinations of individual tree mortality through time and, to date, no detailed on the ground assessments of woodland mortality during the recent drought. Aerial surveys of mortality for blue oak are complicated by the species' adaptive habit of dropping foliage in response to drought, and, while the U.S. Forest Service aerial team did do a special survey of oaks in 2016 and 2017 to confirm increased mortality, the authors of those survey reports indicated that the special survey was not comprehensive and that levels of oak mortality were likely greatly under-reported (Moore et al. 2017, 2018).

In Sequoia National Park, blue oak woodlands are a prominent feature of the foothills portion of the park and represent an often understudied part of the park's landscape. During the drought, oak mortality in and around the park visibly increased, causing concern among park managers about the state of the ecosystem. Therefore, in 2017, we surveyed a representative sample of 30 plots distributed throughout the blue oak woodland alliance to estimate tree mortality during the drought and to capture the current species composition and size structure.

Here, we report the results of the survey and compare them with previous datasets from the park's blue oak woodlands. We find that mortality among oak species appears to have been high during the drought, while non-oak species appear to have been less affected. As a result, oak populations dropped more substantially than other species, but, given the large dominance of blue oak in these ecosystems, relative species structure and composition did not change dramatically.

METHODS

Site Description

Within Sequoia National Park, the blue oak woodland alliance is located in the foothills between 418 and 1462 m in elevation and occupies about 880 ha. The climate is Mediterranean, with hot, dry summers and cool, wet winters. Average annual precipitation is 66 cm, with a mean annual temperature of 17.4°C (Western Regional Climate Center 2018). About 240 ha (27%) of the woodland has been managed as a pasture since at least 1920 (Bartolome et al. 2016). Nine of our 30 sample plots (see below) were located in the pasture. Over the last century, 703 ha of the woodland has burned at least once, but only 22 ha have burned in the last two decades. These more recent fires were prescribed burns initiated by park staff to reduce fuels, generally for the purpose of protecting existing infrastructure. None of our data collection was located in these more recent burns. As an additional precaution, we examined whether there were any relationships between the numbers or proportions of standing dead and the time since last fire and found no significant results. Therefore, we did not consider fire further. Common tree species in the woodland include *Quercus douglasii* Hook. & Arn. (blue oak), *Quercus wislizeni* A. DC. (interior live oak), *Aesculus californica* (Spach) Nutt. (California buckeye), *Fraxinus dipetala* Hook. & Arn. (California ash), and *Cercocarpus betuloides* Nutt. (mountain mahogany).

Data Collection

In the spring of 2017, we surveyed 30 plots (hereafter referred to as 'drought plots') to provide an unbiased characterization of tree mortality, by species and size class, across the blue oak woodlands in Sequoia National Park. Our study area was defined as the blue oak woodland alliance (Fig. 1), as indicated by the park vegetation map. Plot locations were selected *a priori* using Generalized Random Tessellation (GRTS) sampling, which provides a spatially balanced sample that has a true probability design, allowing valid inference for the entire study area (Stevens and Olsen 2004). In the field, plot centers were determined using a proximity alarm on handheld GPS units, with the alarm sounding when proximity to the predetermined GRTS location was within the measurement error of the device. Plots were defined as the area within a 17.84 m horizontal radius (determined by electronic rangefinders) from these plot centers, yielding 0.1 ha sample areas. Precise plot locations were determined using a JAVAD Triumph-2 GPS unit that, after post-processing, determined actual locations with sub-meter accuracy. We attempted to sample 41 plots, but six plots could not be reached safely and five plots overlapped a road, leaving a total of 30 sampled plots for analysis. We failed to get precise GPS coordinate for two plots due

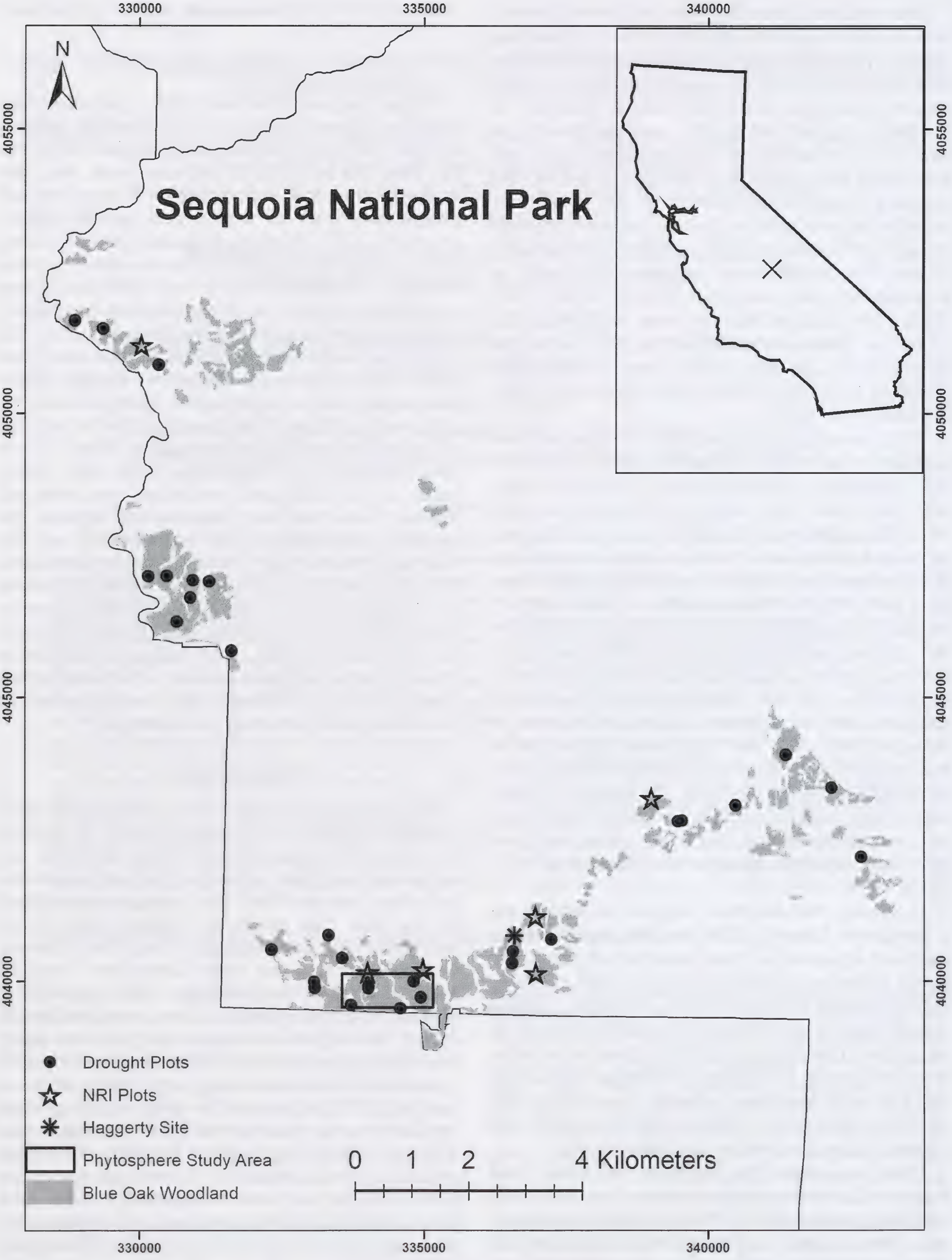

FIG. 1. Map of study area and study sites. Boundary shown on the larger map is the Sequoia National Park boundary. Coordinates are UTM, NAD83, Zone 11N.

to inadequate data collection. For the remaining 28 plots, our plot centers were never more than 10 m from the GRTS target, and the average difference in location was 5.3 m.

Within each plot, we surveyed live trees and standing dead trees that had a trunk diameter at breast height (1.37 m along the length of the trunk) of at least 2 cm. "Standing" was defined as any tree leaning less than 45 degrees from vertical and retaining at least 1.37 m of trunk length. For each tree, we recorded the species, trunk diameter at breast height (DBH; in 5 cm classes), and condition (living or dead). We defined a tree to include any stem that reached breast height regardless of whether it shared a base with another tree (i.e., structural individuals rather than genetic individuals). Dead trees were further classified according to foliage and fine twig retention to provide some indication of which trees had died more recently (see Table S1 in Supplemental Material). Samples sizes and frequency of occurrence (by plot) are given in Table S2.

Comparison Datasets

An issue with rapid 'snapshot' surveys of mortality is that, in the absence of tree rings, it is generally difficult or impossible to determine the exact year of death of standing dead trees, making it a challenge to determine with confidence whether a large number of standing dead trees represents high mortality or low rates of tree fall. Therefore, we identified three existing, pre-drought datasets with data on dead trees from blue oak woodlands in the park and used them for comparison with our drought plot data (Table 1). If drought mortality was high, we would expect the number of standing dead trees estimated from the drought plots to be substantially higher than the number of dead recorded prior to the drought.

Our most robust (in terms of sample size) pre-drought dataset was collected in 1992 as part of a statewide study on the status of blue oak sapling recruitment and regeneration (hereafter referred to as the Phytosphere dataset, after the name of the organization that collected the data). The study used 15 locations throughout the range of blue oak woodlands in California (Swiecki et al. 1993). One of those locations was in Sequoia National Park and was not only in our study area, but overlapped several of the drought plots that were in the pasture (Fig. 1). The Phytosphere data were collected inside a randomly placed sampling grid, which consisted of a series of parallel transects 100 m apart. Plots were placed at 80 m intervals along these transects until 100 plots had been sampled (Swiecki et al. 1993). Plots were circular with a 16 m radius (0.08 ha). Data collection was focused on seedlings and saplings, however, counts of live and dead blue oak trees were also collected, with a tree being defined as any individual at least 3 cm in DBH at 140 cm above ground level. The Phytosphere data included any dead tree that, based on wood degradation, appeared to have died in the last 30 years, regardless of whether it was standing. For this analysis, we have also included their 1 to 3 cm DBH sapling class (which was designated S3 in the Phytosphere data). The Phytosphere data provide a robust estimate of the proportion of dead blue oak in 1992 (although not by tree size).

TABLE 1. DATASET DESCRIPTIONS. Asterisk (*) indicates that only nine of the Haggerty Plots contained trees.

Dataset	Year	# of plots	Plot size (ha)
Drought Plots (Current Dataset)	2017	30	0.10
Phytosphere Plots	1992	100	0.08
NRI Plots	1986–1987	6	0.10
Haggerty Plots	1987	10*	0.05

Methods differed somewhat between our drought plots and the Phytosphere data. The Phytosphere protocol used a slightly taller definition of breast height (140 cm versus 137 cm) and, with the inclusion of the S3 class, a slightly smaller diameter cutoff (1 cm versus 2 cm). This probably results in a trivial overestimate of overall blue oak density relative to our drought plot data, as only 2 saplings fell in the S3 class for the entire Phytosphere dataset. Furthermore, as the drought plot dataset only included standing dead trees, the comparison with the Phytosphere set will be conservative with respect to detecting an increase in mortality during the drought.

The second set of pre-drought comparison data was from the Natural Resources Inventory (NRI) program, which was a park-wide survey of vascular plants in Sequoia and Kings Canyon National Parks (Graber et al. 1993). As part of the program, park staff installed circular, 0.1 ha plots throughout the parks near 1-km UTM grid intersections. Six of those plots fell inside our blue oak woodland study area and were surveyed in 1986 and 1987. As part of the survey, all standing trees, defined as stems at least 1.3 m in height, were recorded and measured for DBH to the nearest 1 cm. Live trees were identified to species, but dead trees were simply identified as 'snags'. These plots provide a pre-drought comparison of standing dead by size class (though not by species). Again, there is a small difference in the definition of breast height which could lead to small discrepancies between datasets.

The third comparison set was from data collected by P. K. Haggerty as part of a study to assess the damage and recovery of blue oak woodland after a wildfire in Sequoia National Park in 1987 (Haggerty 1991, 1994). As part of that study, she used a control site that had not burned. We use that site here as our pre-drought comparison. Data were taken in ten circular, 0.05 ha plots, only nine of which contained trees. In each plot, all standing live and dead trees at least 1.37 m in height were recorded, identified to species, and measured for DBH. Because of limited

TABLE 2. PERCENT STANDING DEAD BY FOLIAGE AND TWIG RETENTION CATEGORY FOR DROUGHT PLOTS. Numbers in parentheses describe the 95% confidence interval of the estimate. The few unexpected small increases in percent of standing dead for the last column are due to changes in the estimation of the random plot effect. A '0' without confidence intervals indicates no dead trees in that sample.

Species	Size class (cm)	Any foliage or fine twig retention	Any foliage retention or fine twig retention in ≥⅓ of the canopy	Any foliage retention or fine twig retention in ≥⅔ of the canopy
Blue oak	All	18.9 (13.6 to 25.8)	16.6 (11.1 to 24.2)	15.7 (10.3 to 23.4)
	2–10	19.8 (9.7 to 36.2)	15.6 (6.7 to 32.0)	16.6 (7.2 to 34.0)
	10–20	17.8 (10.8 to 28.0)	15.4 (8.6 to 26.0)	13.6 (7.4 to 23.8)
	20–40	15.1 (9.7 to 22.8)	13.3 (7.9 to 21.4)	12.6 (7.4 to 20.6)
	≥40	30.1 (18.5 to 45.0)	26.8 (15.3 to 42.7)	26.3 (14.8 to 42.3)
Interior live oak	All	22.6 (15.9 to 31.1)	20.8 (13.6 to 30.5)	20.8 (13.3 to 31.0)
	2–10	13.6 (8.8 to 20.6)	12.1 (7.2 to 19.6)	11.8 (6.9 to 19.5)
	10–20	51.7 (36.4 to 66.7)	49.0 (32.5 to 65.7)	49.3 (32.4 to 66.4)
	≥20	46.6 (28.8 to 65.4)	46.1 (27.1 to 66.3)	46.9 (27.3 to 67.5)
California buckeye	All	4.6 (2.8 to 7.6)	1.7 (0.8 to 3.5)	1.1 (0.4 to 2.7)
	2–10	6 (3.5 to 10.2)	2.3 (1.0 to 5.0)	1.4 (0.5 to 3.5)
	10–20	2.6 (0.8 to 8.4)	1.8 (0.4 to 7.7)	1.8 (0.4 to 7.7)
	≥20	0.9 (0.1 to 6.8)	0	0
California ash	All	4.9 (2.1 to 11.1)	3.3 (1.2 to 8.8)	3.8 (1.3 to 10.2)
Other	All	10.5 (5.7 to 18.7)	9.4 (4.8 to 17.7)	9.9 (5.0 to 18.9)

sample sizes, we were only able to use blue oak for purposes of comparing mortality with our current dataset.

Analyses

In order to assess the level of mortality during the drought, we compared the number of dead trees between pre-drought datasets and our drought dataset. We also estimated the proportion of recent dead (based on foliage and twig retention) in the drought dataset. Finally, we examined apparent changes in species composition due to mortality during the drought.

We separately examined any species with at least 100 stems in our drought plot dataset, lumping the rest into an 'Other' category. To examine size structure and species composition, we divided the trees within a species into the following DBH classes: ≥2 and <10 cm, ≥10 and <20 cm, ≥20 and <40 cm, and ≥40 cm. We assessed composition within these species and size class combinations before and after likely recent mortality to examine drought induced changes in composition. For mortality analyses, we required a minimum of 30 trees within a species and size class. Therefore, when necessary, we lumped adjacent size classes for mortality analyses to achieve adequate sample sizes.

We estimated mortality (i.e., proportion of standing dead) using generalized linear mixed effect models with a binomial distribution and a logit link (i.e., a mixed effects logistic regression). Species or the combination of species and size class (with each species and size class combination considered as a separate category) were used as categorical predictors, and plot identity was used as the random effect. We estimated the proportion of standing dead for both all dead trees and for apparently recently dead trees. Recently dead trees were defined as those retaining any leaves or fine twigs (though we also analyzed the data using more strict definitions of recently dead as shown in Table 2). For other datasets, we only estimated all dead (Phytosphere dataset) or standing dead, as we did not have data on leaf or twig retention. Because information depth varied by dataset (e.g., size class, species identity), we performed additional analyses as necessary on our drought plot data in order to match those from the comparison sets.

We estimated the average species and size composition by fitting negative binomial models, with count of trees within a plot as the dependent variable and species or species and size class combination as categorical predictors. Due to the highly variable spatial structure of these woodlands, means and medians often differed substantially. For example, certain species occurred infrequently in our plots but, when they occurred, were present in high numbers (Table S2), leading to a relatively high average but a very low median.

All analyses were performed in R 3.1.1 using the *MASS* and *lme4* packages (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

All Dead

Our estimates of the proportion of standing dead trees in the drought plots, 18.4% (95% CI = 13.7–24.2) of all standing trees and 22.7% (95% CI = 17.0–29.5) of standing blue oak, were three to five times higher than estimates of dead trees from any of the pre-drought comparison datasets (Table 3, Table S3). This was also true within size classes (Table 3,

TABLE 3. PRE-DROUGHT MORTALITY COMPARISONS. The data in this table include all dead trees, rather than just those that still retain foliage and fine twigs (i.e., those that have likely died more recently). The numbers in parentheses are 95% confidence intervals. The Haggerty and NRI datasets included only standing dead trees. The Phytosphere dataset also included fallen dead trees. Asterisk (*) indicates a subset of landscape plots (six plots in total) that occur in or near the Phytosphere study area.

Pre-drought comparison dataset	Type of dead	Pre-drought dead (%)	Drought standing dead (%)
Phytosphere (all sizes)	Blue oak	5.2 (4.1–6.5)	22.7 (17.0–29.5) 25.7 (17.0–36.8)*
Haggerty (all sizes)	Blue oak standing	7.6 (3.4–16.2)	22.7 (17.0–29.5)
Haggerty (2–<20 cm)	Blue oak standing	4.4 (1.4–13.0)	26.4 (17.8–37.2)
Haggerty (≥20 cm)	Blue oak standing	15.2 (6.5–31.6)	23.4 (16.5–32.0)
NRI (all sizes)	All standing	3.9 (1.6–9.0)	18.4 (13.7–24.2)
NRI (2–<20 cm)	All standing	3.0 (0.7–11.2)	16.8 (12.3–15.3)
NRI (≥20 cm)	All standing	4.9 (1.6–14.2)	21.1 (15.3–28.0)

Table S4), with the exception of large blue oak in the Haggerty dataset where confidence intervals from our drought plots and pre-drought data overlapped. In the case of the Phytosphere data, we were also able to compare results against a subset of our drought plots that occurred within or near the Phytosphere study area and found our estimates for the proportion of standing dead trees, 25.7% (95% CI = 17.0–36.8), to be nearly five times Phytosphere estimates of dead trees from prior to the drought. This is an especially notable increase, given that the Phytosphere data included both standing and fallen blue oaks. These results are also consistent with numbers from two recently installed long-term monitoring plots in the park (Appendix 1), where the proportion of all standing dead were 34.2% (95% CI = 27.5–41.6) and 15.0% (95% CI = 11.6–19.2) and the proportion of blue oak standing dead were 34.0% (95% CI = 27.4 41.4) and 20.4% (95% CI = 16.7–24.7).

Recently Dead

Since our pre-drought standing dead estimates are from data collected two to three decades prior to the drought, an alternative explanation for the increase in standing dead might be a more gradual accumulation of standing dead over a period of many years rather than a spike during the recent drought. While this seems unlikely, as it would also imply a substantial change in the fall rate of dead trees, we also analyzed standing dead for our drought plots based on foliage and twig retention, as trees that retain foliage and twigs presumably died more recently. If we restrict our analysis only to live trees and dead trees that have retained foliage or fine twigs (Table 2, Fig. 2), we find that the numbers of standing dead are still high relative to pre-drought datasets, with 14.0% (95% CI = 9.7–19.9) of all trees being recently dead. For oak species, recently dead trees account for 18.9% (95% CI = 13.6–25.8) and 22.6% (95% CI = 15.9–31.1) of standing blue oak and interior live oak respectively (Fig. 2, Table 2, Table S3). Recent mortality was also high among 'Other' species (10.5% [95% CI = 5.7–17.7] of standing stems), driven primarily by mortality in canyon live oak (*Quercus chrysolepis* Liebm.), which is at the lower end of its elevational range in blue oak woodland and occurs only rarely. In contrast, only 4.6% (95% CI = 2.8–7.6) of California buckeye and 4.9% (95% CI = 2.1–11.1) California ash trees appear to have died recently.

For blue oak, interior live oak, and California buckeye, our sample sizes of more recently dead trees were large enough for analyses by size class. Recent blue oak mortality was high across all size classes, with a higher average mortality rate in trees greater than 40 cm DBH (Fig. 3, Table S4), although there is considerable overlap in the confidence intervals among size classes. Interior live oak had substantially higher mortality rates for trees greater than 10 cm in DBH. California buckeye had low mortality across the size classes, with some indication of decreasing

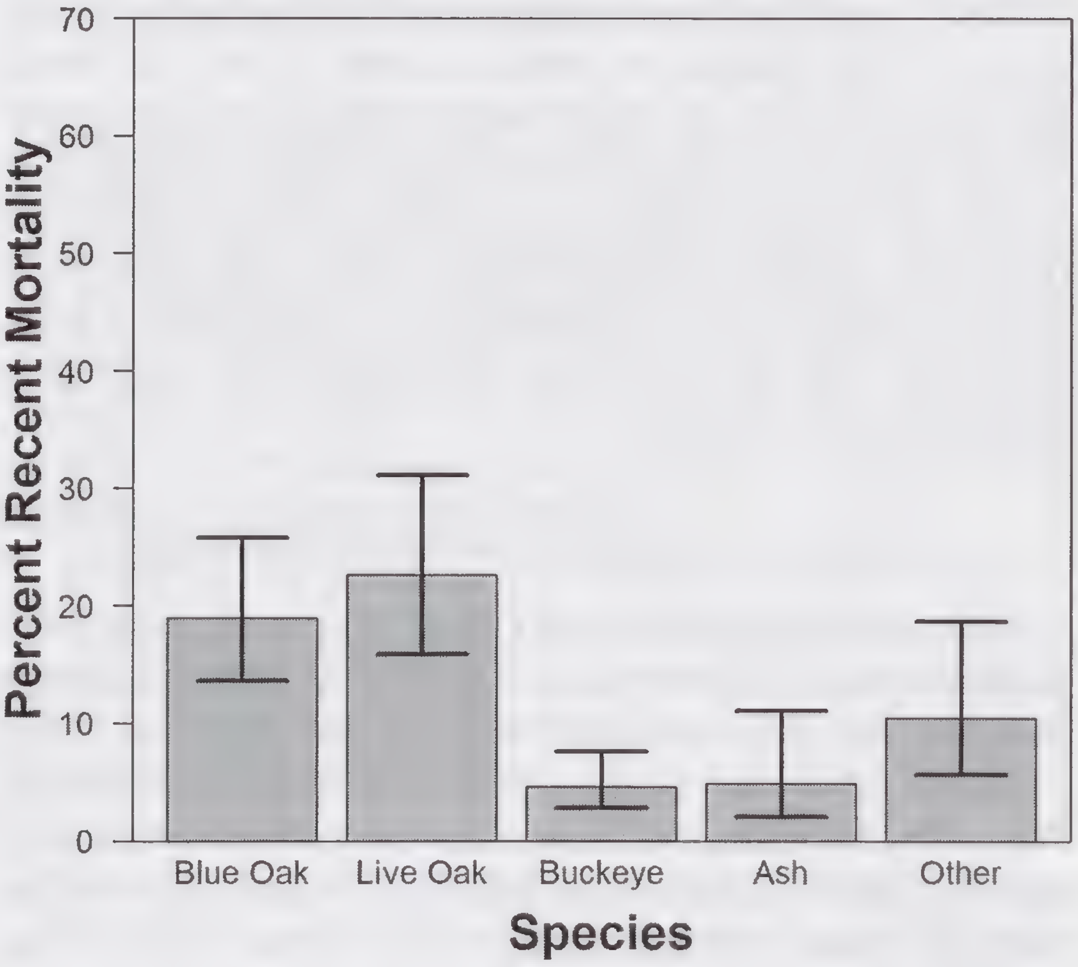

FIG. 2. Percent recent mortality by species in the drought plots, obtained by restricting the drought plot dataset to live trees and recently dead trees. Recently dead trees were defined as standing dead trees that retain foliage or fine twigs. Error bars are 95% confidence intervals.

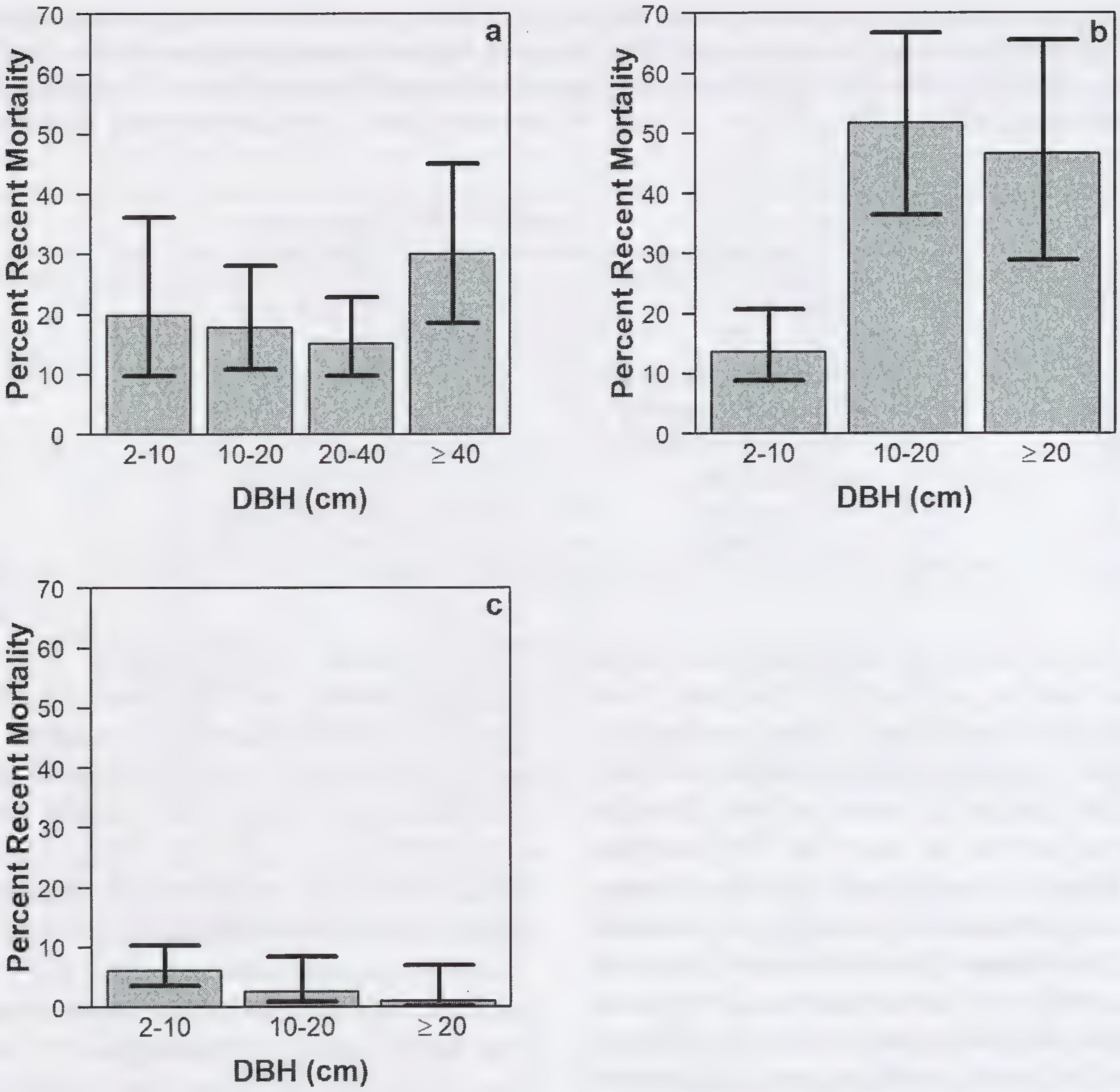

FIG. 3. Percent of recent mortality by size class for a) blue oak; b) interior live oak; and c) California buckeye. Error bars are 95% confidence intervals. Estimates were obtained by only considering live and recently dead trees in the drought plot dataset. Recently dead trees were defined as standing dead trees that retain foliage or fine twigs.

mortality with size. However, any size-related trends in buckeye mortality are obscured by the relatively large confidence intervals for this species.

These numbers do not change substantially if we further restrict our sample to standing dead that either retain foliage or retain at least ⅓ or ⅔ of their fine twigs (Table 2), again suggesting that a majority of the standing dead trees have died recently. In addition, these results are consistent with estimates from our recently installed long-term plots, where we find a similarly high occurrence of standing dead blue and live oak with foliage and fine twig retention (Appendix 1, Fig. S1).

Species Composition and Size Structure

Unsurprisingly, blue oak dominates these woodlands in basal area (Fig. 4, Table S5), with most blue oak stems being in the $\geq$20 to <40 cm size class (Fig. 5, Table S6). This dominance remains even after the substantial apparent losses due to mortality during the drought, with average blue oak basal area in our drought plots dropping by 26%, from 9.5 m^2/ha (95% CI = 7.4–11.6), when including live and recently dead trees, to 7.0 m^2/ha (95% CI = 5.3–8.7), when only including live trees.

While the average number of interior live oak and California buckeye are higher than the average number of blue oak (Fig. 4, Table S5), their stems tend to be small (Fig. 5, Table S6) and occur only in rare, dense patches, hence the large disparity between mean and median densities for these species. In contrast, small blue oak are found only rarely (Fig. 5). Overall, median blue oak density is much higher than all other species combined. Importantly, in this study, we counted structural individuals (ramets) rather than genetic individuals (genets), and many of the interior live oak, California buckeye, and California ash stems are from small clumps of stems that originate from the same base.

DISCUSSION

Mortality

Aerial surveys suggest that recent drought mortality in the blue oak woodlands of California has been high (Moore et al. 2017). Our data in Sequoia National Park bear out that assessment, indicating far higher numbers of dead trees after the onset of the drought than prior to it, with nearly 20% of standing blue oak apparently having died recently. Mortality rates appear to have been even higher among interior live oak, while other major woodland species appeared less affected.

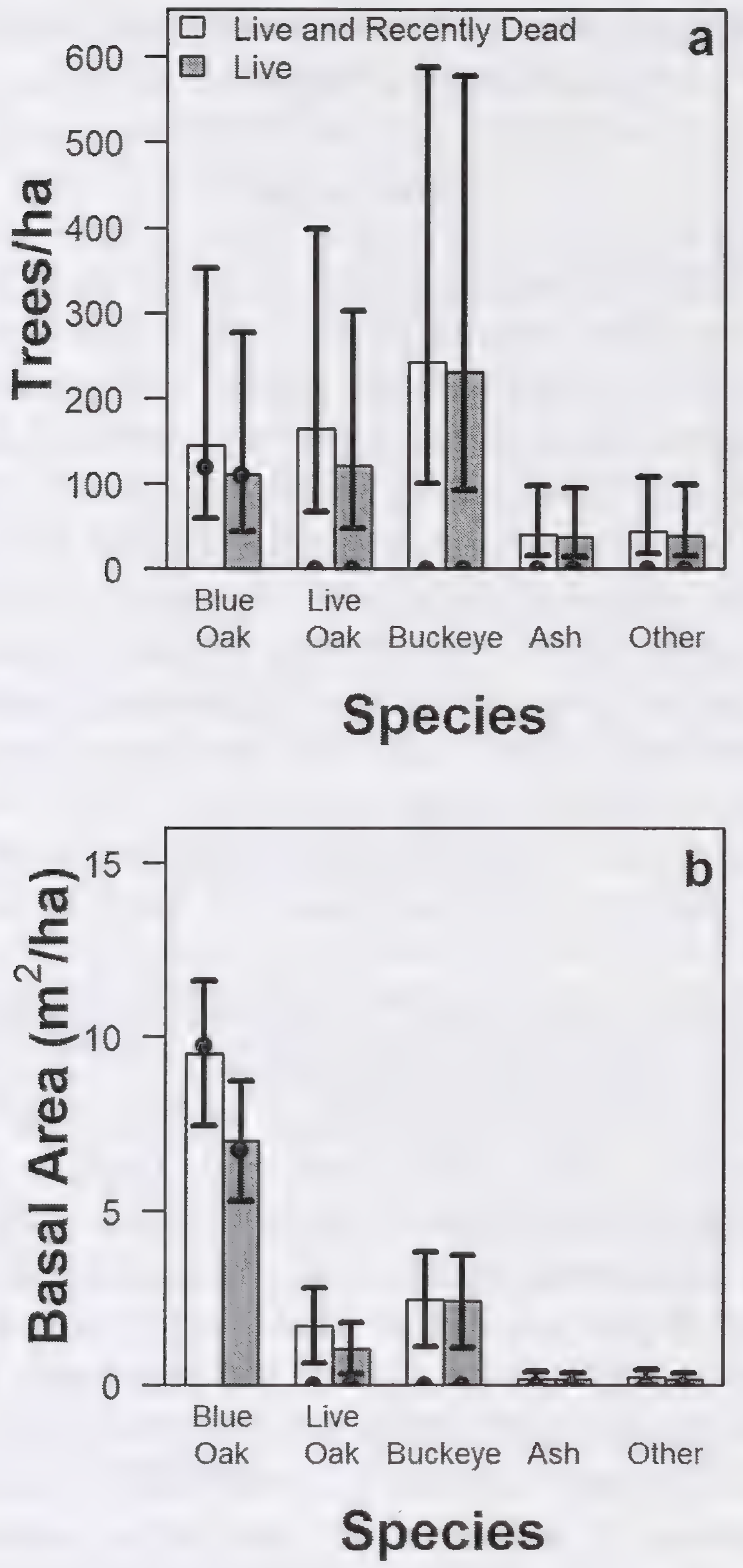

FIG. 4. Blue oak woodland composition, including a) average density and b) average basal area by species for living and recently dead trees combined and living trees alone. Recently dead trees are defined as those dead trees that retain foliage or fine twigs. The combination of living and dead trees can be considered as an estimate of living trees prior to drought mortality. Error bars are 95% confidence intervals. Black dots are medians.

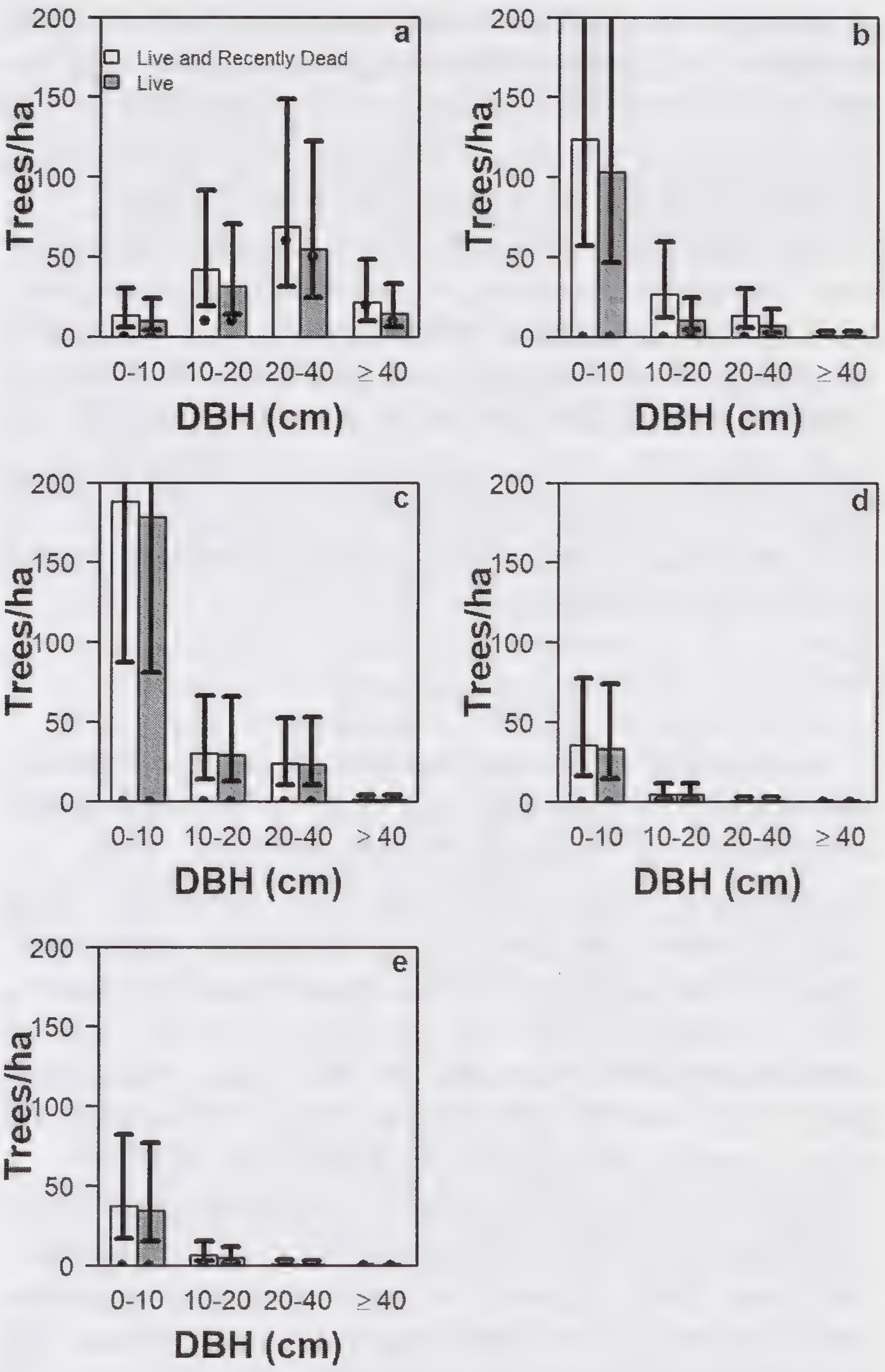

FIG. 5. Average density by size class for live and recently dead trees combined and live trees for a) blue oak, b) interior live oak, c) California buckeye, d) California ash, and e) Other species (see main text), as estimated from the drought plots. Recent mortality is defined as standing dead trees that retain foliage or fine twigs. Error bars are 95% confidence intervals. Black dots are medians.

This assessment is further supported by blue oak woodland data from other parts of California, which show that blue oak woodlands typically had much smaller pre-drought populations of dead trees than we found in our drought plots. For example, for all 15 sites from across California in the full Phytosphere dataset (Swiecki et al. 1993), dead blue oak varied between 2.3% and 10.8% of all trees, with an average of 5.9%, even including both fallen and standing dead. This compares to 25.7% for our drought plots, which only include standing dead. A nest site study at the San Joaquin Experimental Range in the Sierra Nevada in the 1980s reported 1.1% and 1.2% of standing trees with a DBH > 8 cm (all species) were dead in their two plots (Waters et al. 1990), and another habitat study in San Luis Obispo, CA in 1995 found that standing dead comprised between 6.7 and 8.8% of standing trees with DBH ≥ 5.1 cm (Tietje et al. 1997). These numbers compare to 19.7% or 23.9% for lower size limits of 5 cm and 10 cm respectively in our plots. Finally, in a recent study on the effect of mistletoe on California oaks (Koenig et al. 2018), of a set of 257 blue oak trees, mostly greater than 20 cm DBH and all of which had been tracked since at least 1999, only 6 trees (2.3%) had died as of 2016, suggesting a low mortality rate over a long time period. However, the results do not indicate high mortality among these sample trees during the drought.

Overall, the weight of evidence strongly suggests that the recent drought has dramatically increased (probably quadrupling) the number of dead trees in blue oak woodlands in Sequoia National Park, particularly among oak species.

Surprisingly, our estimates of mortality for the other relatively abundant species, California buckeye and California ash, were much lower than for oak species. Unfortunately, we are not aware of any other studies assessing mortality or relative drought tolerance for buckeye and ash. In the case of ash, the lack of apparent response may be a tendency for the species to prefer riparian areas, perhaps biasing occurrence to parts of the landscape with higher moisture availability. That said, our sample size for ash was modest, and the species only occurred in 5 of our 30 plots (Table S2). Therefore, our ash mortality estimates should be treated with some caution.

For buckeye, we had a robust sample (794 trees), and the species occurred in over 40% of our plots, making our estimates of mortality less prone to sampling error. Furthermore, there was little visual evidence of elevated mortality among buckeye in the park generally. This suggests that buckeye may simply be more drought tolerant than either of the oak species, though such a determination would require further research.

Composition

Recent mortality has clearly reduced the biomass and density of blue oak and interior live oak in the woodlands at Sequoia National Park (Fig. 4). Nonetheless, even accounting for mortality, blue oak remained the dominant species by basal area and, for trees >10 cm DBH, by density. In contrast, and in keeping with the well-documented lack of recruitment for blue oak in blue oak woodlands generally, smaller size classes were dominated by other species, both before and after the drought.

While our analyses focused on standing dead trees, estimates of overall composition from all the Sequoia National Park datasets we used were fairly consistent. Estimates of blue oak densities from the Phytosphere, Haggerty, and NRI datasets were 159 trees/ha, 212 trees/ha, and 98 tree/ha respectively, all well within the uncertainty range of the density estimates of live and recently dead trees from our landscape dataset (Fig. 4). These estimates are also consistent with the data used to develop the vegetation map in the parks, which gave an estimate for blue oak density of 115 trees/ha. We did not use this last dataset in our main analysis because it lacked information on dead trees. Note that, as described in the Methods, there are small differences in DBH cutoffs among our datasets, which in some circumstances can result in large differences in density estimates. That said, for blue oak, due to the low abundance of saplings and smaller trees, these small discrepancies in DBH cutoffs are unlikely to have had a substantial effect.

All of these results are in stark contrast to those reported by Vankat and Major (1978) and Roy et al. (1999), who estimated average blue oak densities in the park at 600 trees/ha or more. This is well outside the 95% confidence interval of our estimate of average density from our data and is, in fact, outside the entire range of densities from our plots (Fig. 4b). Moreover, the estimate differs substantially from those obtained from every other dataset collected in blue oak woodlands in the park. This difference is almost certainly a result of a bias in the Vankat and Major (1978) and Roy et al. (1999) datasets, including possible 'majestic forest bias' and a bias in their sampling design (Appendix 2).

Conclusions

Our surveys suggest that a substantial percentage of canopy blue oak in Sequoia National Park died during the drought, and, given indications from aerial data, this is likely a pattern repeated in many blue oak woodlands, particularly in the southern half of their distribution in California (Brown et al. 2018). But while the mortality was substantial and particularly concentrated within oak species in our study area, this has not changed the general character of the woodland. Blue oaks still dominate our study landscape, and the large majority of trees survived. In other words, drought mortality, while dramatic, has not led to type conversion, at least in the short term.

However, in the longer term, such mortality events may have important consequences. As documented above, there is ample evidence that blue oaks are not regenerating at a rate that can sustain existing populations, even without massive losses. Our results indicate that nearly a fifth of the blue oaks in Sequoia National Park may have died during the drought, without much prospect for replacement. If such droughts occur with increased frequency (e.g., Allen et al. 2010) and without a concomitant increase in regeneration, blue oaks could decline in prominence.

How the effects of increased drought frequency and severity play out across the range of blue oak woodlands will likely vary by locale. The blue oak stand at Sequoia National Park was among the most xeric of the 15 blue oak locations included in the Phytosphere data, due to a combination of high insolation, low soil available water holding capacity, and high evapotranspiration relative to annual precipitation (Swiecki et al. 1993). In xeric locations, blue oak regeneration tends to be restricted to the most mesic sites, such as north-facing slopes, patches of deeper soil, and wetter topographic positions (Swiecki and Bernhardt 1998). Changes in climate that further increase evapotranspiration or result in longer and more severe droughts are likely to further limit the likelihood that gaps created by overstory blue oak mortality will be filled by blue oak advance regeneration. The expected result is that blue oak would continue to decline at xeric locations such as this. In more mesic locations, blue oak recruitment is more likely to be limited by dense canopies of competitors, such as interior live oak, and tends to be restricted to more xeric sites where competition with less drought-tolerant species is reduced. In mesic locations, especially in the wetter northern portion of its range, blue oak may have more opportunities for recruitment in a warmer and drier climate if its less drought tolerant competitors are suppressed. Furthermore, the recent drought was most severe in the southern part of the blue oak range (e.g., Williams et al. 2015), so drought-related mortality may also be less intense in more mesic locations.

Blue oak woodlands are an important and iconic part of the California landscape. Our work here, combined with decades of previous work on blue oak regeneration, support the contention that these ecosystems may be particularly vulnerable in a warming climate. Going forward, it behooves us to give these woodlands increased attention, including effective and consistent monitoring of adult trees. Such information is likely to be critical not only for understanding changes in these woodlands, but also for informing management decisions, whether intended to boost resilience in these systems or to facilitate change.

ACKNOWLEDGEMENTS

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APPENDIX 1

LONG-TERM MONITORING PLOTS

While several research and monitoring projects have been located in blue oak woodlands over the history of Sequoia National Park, no ongoing or systematic assessment of the woodlands' conditions had been conducted in many years. To help fill this gap, in addition to the drought plots described in the main text, we established two 2.25-ha permanent plots (named 'BOF' and 'DOP') that will be used for long-term population monitoring and as a venue for citizen science. These plots were not randomly located. Instead, we chose accessible locations with an abundance of blue oak. Both plots are located in Sequoia National Park's pasture area (see Methods). Accessibility was critical to ensure that long-term monitoring is feasible, especially given that much of the future monitoring may rely on volunteers. We chose areas with abundant blue oak so that we had an adequate population for tracking trends. For the BOF plot, average slope was 8.4°, ranging from 2° to 21°, and average aspect was 171°, ranging from 3° to 348°. For the DOP plot, average slope was 13.5°, ranging from 3° to 25°, and average aspect was 118°, ranging from 0° to 352°. Slope and aspect were obtained using GIS layers provided by Sequoia National Park.

The long-term plots are square, with 150 m sides (errors in mapping resulted in the plots deviating modestly from perfect squares). Mapping of plot boundaries and trees was accomplished using the GPS and rangefinder on a Trimble Geo 7X handheld with a Zephyr Model 2 antenna. Every living tree inside the plot boundaries with a diameter at breast height (DBH) $\geq$ 2 cm was tagged, mapped, measured for diameter, and identified to species. In addition, in order to provide a comparison between the long-term and our drought plots, we surveyed all the standing dead trees using the same protocol as within the drought plots. Going forward, long-term plots will be visited every year to check for mortality and to map and measure recruitment. Trees that die will be evaluated for factors associated with mortality (e.g., beetles, fungal pathogens, suppression), and we will record any conditions on live trees that might contribute to future mortality (see Das et al. 2016). Every five years, every living tree will be re-measured for diameter.

In order to compare mortality and composition between our drought and long-term plots, we needed to describe variability within the long-term plots in a way that was comparable to the 0.10 ha drought plots. This required subdividing each long-term plot into smaller subunits. As there is not a simple method for splitting a 150 m X 150 m plot into precisely 0.10 ha plots without excluding a substantial portion of the plot or resorting to very odd combinations of plot shapes, we instead split each long-term plot into twenty-five 0.09 ha square subplots (30 m x 30 m). These subplots vary in size somewhat, as the established plots were not precisely square, but all of the subplots deviate by less than 10% from 0.09 ha.

Mortality patterns in the long-term plots reflected the broader landscape pattern indicated by the drought plots. For the BOF and DOP plots respectively, the proportion of all standing dead were 34.2% (95% CI = 27.5–41.6) and 15.0% (95% CI = 11.6–19.2), and the proportion of blue oak standing dead were 34.0% (95% CI = 27.4%–41.4%) and 20.4% (95% CI = 16.7–24.7). Likely recent mortality (including trees with foliage or fine twig retention) was also high for blue oak in the long-term plots, with a mean of 30.1% at BOF and 18.5% at DOP (Fig. S1a). In the DOP plot, where sample sizes of California buckeye and California ash were adequate for analysis, we found low mortality rates (0.8% and 2.0% respectively, Fig. S1a), in keeping with the pattern on the broader landscape. Mortality of 'Other' species was very high (33.3%, Fig. S1a) in the DOP plot, even compared to the broader landscape, and this high mortality was entirely within the population of mountain mahogany in the plot. Sample sizes of interior live oak were too small to analyze formally in either long-term plot, but 35% of the 40 interior live oak stems that occurred in the long-term plots were dead. Mortality of blue oak was high across size classes (Fig. S1b), although sample sizes in the smallest and larger size classes were limited.

Both of our long-term plots have higher blue oak densities and basal areas than our estimates for the landscape as a whole from the drought plots (Figs. S2 and S3), although variability across the landscape and within the long-term plots is large. As with the drought plots, our long-term plots are dominated by blue oak, with most of the blue oak concentrated in the middle size classes (Fig. S4). Live oak and other species occurred less frequently in our plots than the landscape as a whole, with the BOF plot being nearly exclusively populated by blue oak. The DOP plot had a relatively high concentration of California ash compared to the landscape, but California ash was still a small component of the overall species composition.

Overall, the similarity in mortality patterns between our long-term and drought plots suggest that these plots might serve as reasonable representatives of mortality rates as they are monitored into the future. However, they are probably not effective guides to species composition or changes in species composition through time. Not surprisingly, given our selection criteria, blue oaks appear to be more dense in the long-term plots than the landscape as a whole, and other, smaller-stature species occur less frequently than the average.

Nonetheless, the long-term plots should serve as excellent sentinels for detecting large-scale changes in blue oak populations (particularly increases in mortality rate), and, as venues for citizen science, they have already demonstrated great potential, with National Park Service staff already leading several volunteer groups to measure and re-measure tree diameters. At the very least, they can serve as a key component in an effective monitoring program of blue oak woodlands at Sequoia National Park.

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APPENDIX 2

BIAS IN VANKAT AND MAJOR (1978) AND ROY ET AL. (1999) DATASETS

Blue oak density estimates from Vankat and Major (1978) and Roy et al. (1999) are almost certainly gross overestimates, given the large disparity between their estimates and those from all other blue oak woodland datasets collected in the park. The cause of this overestimation is probably due in part to "majestic forest bias", since the Vankat plots were placed subjectively and such placement can easily fall prey to choosing locations with higher than average densities (e.g., Phillips et al. 2004). Simply placing plots to include several blue oak trees– instead of the single tree that they might have expected with random placement of their 0.01 ha plots– would lead to large overestimates, since each additional tree would add 100 trees per hectare.

In addition, there is a bias in their sampling design that would be synergistic with a majestic forest bias. Vankat and Major (1978) and Roy et al. (1999) used band transects to estimate density, including any tree "rooted" inside the transect, regardless of whether the center of the tree fell within the transect and without any procedure for eliminating overestimation due to such "boundary trees". For example, in order to avoid overestimates, it is common practice to only include boundary trees on one side of the transect (i.e., half the boundary trees) or to only include boundary trees whose center falls within the plot. Lacking such procedures could easily lead to large overestimates, given, as noted above, that each extra tree adds 100 trees per hectare to their estimates. Being 2 m by 50 m, their transects had a high edge to area ratio and therefore would have been particularly prone to including edge trees.

Roy et al. (1999) acknowledge the sampling bias, suggesting that it might lead to "slight" overestimates of basal area, but they provide no explanation for why they think the bias would be slight. In fact, the basal area estimates provide an additional clue. Vankat and Major (1978) report basal area estimates obtained by using wedge prisms, a plotless estimator that would not be subject to edge bias. They reported a basal area estimate of 11.85 m^2/ha for blue oak in blue oak woodlands in 1969, which is consistent with our own basal area estimates (Fig. 4, main text). Roy et al. (1999), however, calculated basal area using plot data, including recalculating it for the Vankat and Major (1978) data from 1969. This recalculation gave an estimate of 21 m^2/ha, nearly double the prism estimate for the same time period.

Unfortunately, one would expect these biases throughout their dataset, making their estimates of density unreliable for all forest types in the parks.

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SILENE NELSONII, A NEW LARGE-FLOWERED SPECIES FROM THE TRINITY RIVER AREA OF NORTHWESTERN CALIFORNIA, USA, AND A RE-EVALUATION OF *S. BOLANDERI* GRAY

MICHAEL R. MESLER
Department of Biological Sciences, Humboldt State University, Arcata, CA 95521
mrm1@humboldt.edu

MICHAEL S. MAYER
Department of Biology, University of San Diego, San Diego, CA 92110

SYDNEY K. CAROTHERS
Department of Biological Sciences, Humboldt State University, Arcata, CA 95521

ABSTRACT

Silene nelsonii M.R. Mesler, M.S. Mayer, and S.K. Carothers (Caryophyllaceae), a species with large, day-blooming flowers from the Trinity River Basin of northwestern California, is described and illustrated. In the past, plants assignable to this new species have been referred to incorrectly as *S. bolanderi* A.Gray or *S. hookeri* Nutt. subsp. *bolanderi* (Gray) Abrams, names that rightfully apply to another member of the *Silene hookeri* complex. Here we argue that both *S. nelsonii* and *S. bolanderi* are worthy of recognition as separate species based on morphological distinction and a molecular phylogenetic analysis. *Silene nelsonii* differs from *S. bolanderi* by its more deeply lobed, white petals; lack of well-developed coronal petal appendages; densely ciliate petal bases; and shorter, sometimes branched sepal hairs. We present a key to the five members of the *S. hookeri* complex, all of which are in some degree rare in California and worthy of conservation concern.

Key Words: Caryophyllaceae, *Silene*, Trinity River, new species, rare.

Nuttall described *Silene hookeri* Nutt. in 1838 based on a type specimen collected near Portland, Oregon (Nuttall s.n., BM000582593!), and since then the name has been applied broadly to a group of low-growing perennials from western Oregon and northwestern California with large, ± upright, day-blooming flowers with four-lobed petals (Hitchcock and Maguire 1947; Munz and Keck 1959; Peck 1961). Subsequent authors described five additional species for the group, based on differences in flower size, petal color, pattern of petal lobing, presence/absence of coronal petal appendages, degree of glandularity, and degree of stamen exsertion. These species have been variously accepted, placed in synonymy, reduced to subspecies, or ignored in recent treatments (Table 1). For example, Asa Gray named *Silene bolanderi* (A.Gray) in 1868 based on specimens collected by Henry Bolander near Laytonville, in Mendocino County, California (*Bolander 4696;* holotype, GH00037857!). In his field notebook, Bolander described the plants as "... the finest species met with yet...[with] ...flowers of a very delicate pink color, large and showy." Gray regarded the species as "very...distinct" (Gray 1868), but later authors have disagreed about its status. Some included it as an un-named part of a broadly circumscribed *S. hookeri*, which also has pink flowers (Hooker 1873; Gray 1878; Watson 1880; Jepson 1925; Wilken 1993), while others treated it as a subspecies of *S. hookeri* (Abrams 1944; Hitchcock and Maguire 1947; Munz and Keck 1959; Smith and Wheeler 1990–1991; Morton, 2005). Recently, Hartman et al. (2012) resurrected the taxon as a distinct species in *The Jepson Manual*, 2nd ed. based on evidence presented by Nelson and Nelson (2004), a position adopted in the second volume of *Flora of Oregon* (Rabeler and Hartman, in press).

Our interest in the *S. hookeri* complex was motivated by examination of plants from Burnt Ranch, Trinity County, CA, whose white flowers have impressively long, narrow petal lobes and lack well-developed coronal petal appendages. These plants key to *S. bolanderi* in *The Jepson Manual*, 2nd ed., but our field and lab work has convinced us they do not match Gray's description of *S. bolanderi* or the type collection, which has pink petals and petal appendages. Here we describe the white-flowered plants as a new species, *S. nelsonii*, and present morphological and molecular phylogenetic evidence to show that it is worthy of recognition. We also argue that plants from Humboldt, Mendocino, Trinity, and Josephine counties that *do* match the original description of *S. bolanderi* represent a distinct species, separate from *S. hookeri*, and we present a key to the members of the *S. hookeri* complex.

TAXONOMIC TREATMENT

Silene nelsonii M.R.Mesler, M.S.Mayer, & S.K.Carothers, sp. nov. (Figs. 1, 2, 5). – TYPE: USA, California, Trinity Co., 2.4 mi SW of Burnt Ranch, 0.75 mi from junction with FS 60 along FS 5N40, openings in mixed-age conifer forest, 25

TABLE 1. Varying opinions about the taxonomic treatment of the *Silene hookeri* complex. "+" = taxon recognized at the same level; "-" taxon neither recognized nor placed into formal synonymy; † = treatment published before taxon name.

	Jepson (1925)	Abrams (1944)	Hitchcock and Maguire (1947)	Munz and Keck (1959)	Peck (1961)	Morton (2005)	Hartman et al. (2012)	Rabeler and Hartman (2019)
Silene hookeri Nuttall ex. Torrey & Gray (1838)	+	*S. hookeri* spp. *hookeri*	*S. hookeri* spp. *hookeri*	*Silene hookeri* ssp. *hookeri*	+	*S. hookeri* spp. *hookeri*	+	*S. hookeri* ssp. *hookeri*
S. bolanderi Gray (1868)	-	*S. hookeri* ssp. *bolanderi*	*S. hookeri* ssp. *bolanderi*	*S. hookeri* ssp. *bolanderi*	-	*S. hookeri* ssp. *bolanderi*	+	+
S. ingramii Tidestrom and Dayton (1929)	†	-	*S. hookeri* spp. *hookeri*	restricted to OR	+	-	-	-
S. pulverulenta Peck (1932)	†	-	*S. hookeri* ssp. *pulverulenta*	restricted to OR	+	-	restricted to OR	*S. hookeri* ssp. *hookeri*
Silene serpentinicola Nelson & Nelson (2004)	†	†	†	†	†	+	+	*S. hookeri* ssp. *serpentinicola*
Silene salmonacea Nelson, Nelson, & Erwin (2006)	†	†	†	†	†	†	+	restricted to CA

May 2015, *M. R. Mesler 1642* (holotype: HSC; isotypes: UC, OSU, MICH).

Diagnosis: Silene nelsonii differs from *S. bolanderi* by its more deeply lobed white petals, lack of well-developed coronal petal appendages, relatively short, sometimes branched calyx hairs, and by its densely ciliate petal bases. *Silene nelsonii* differs from *S. hookeri* by its flaring, more deeply and more equally lobed petals, lack of well-developed coronal appendages, its radially symmetrical androecium, and densely ciliate petal bases.

Description: Perennial herbs; flowering shoots 2.5–25 cm tall, solitary or often in large clusters, arising at the tips of slender bracteate, rootless, branched or unbranched horizontal to ascending rhizomes that radiate from the crown of a deep taproot; aboveground stems simple to 1-branched, erect to decumbent, 0.6–22 cm long (not including pedicel of central flower), internodes 0.1–6.5 cm long, green to gray-green, sparsely pubescent to densely canescent, hairs simple, eglandular, straight or curled; lowermost leaves green, small, bract-like, +/- at ground-level, 2–17 mm long, 1.3–3.7 mm wide, 2–4 pairs of larger, larger cauline leaves above, green to gray-green, crowded to widely separated (in shade), petiolate or sessile, the largest subtending the inflorescence, 21.8–81.8 mm long, 5.8–18.9 mm wide, blade elliptic or oblanceolate to obovate, apex acute, base tapering to a +/- distinct petiole or not; inflorescence a 2–4 (7)-flowered cyme or flowers solitary, pedicels erect to ascending, canescent, eglandular, 0.5–7.5 cm long, deflexed in fruit, lowermost pair of bracts elliptic to narrowly oblanceolate, nearly as large as upper pair of cauline leaves, 13.9–61.0 mm long, 2.1–12.0 mm wide; flowers erect to ascending, 2.8–5.5 cm long, 2.5–6.8 cm wide, sometimes +/- as large as the aboveground vegetative body, diurnal, not fragrant, protandrous; calyx white-green or gray-green, 10-nerved, narrowly cylindric to clavate-obovoid, usually widest at or just above midpoint, narrowed at base of lobes, 11.8–23.5 mm long, 4.7–9.0 mm wide, expanded in fruit, base rounded or truncate, lobes narrowly triangular, acute to narrowly acute, sparsely to densely canescent, hairs simple or forked at base, eglandular, +/- opaque, straight or curled, sharp; anthophore pale green or white, glabrous, 1.3–5.0 mm long, 1.3–1.8 mm wide, length:width ratio 1.0–2.0; corolla narrowly to broadly funnel-shaped, white with a broad, translucent pale gray-green throat; petals initially ascending [early male stage], becoming recurved [late-male, female stage], not sharply bent at intersection of claw and limb, 20.2–50.0 mm; coronal appendages absent or present as inconspicuous white teeth, ≤1 mm long; claw longer than calyx, 12–23 mm, narrow at base, gradually expanded upward, translucent pale gray, with 2 +/- low white ribs, margin densely ciliate at base, hairs +/- obscuring gap between claw bases and antisepalous filaments; limb white, much wider than claw,

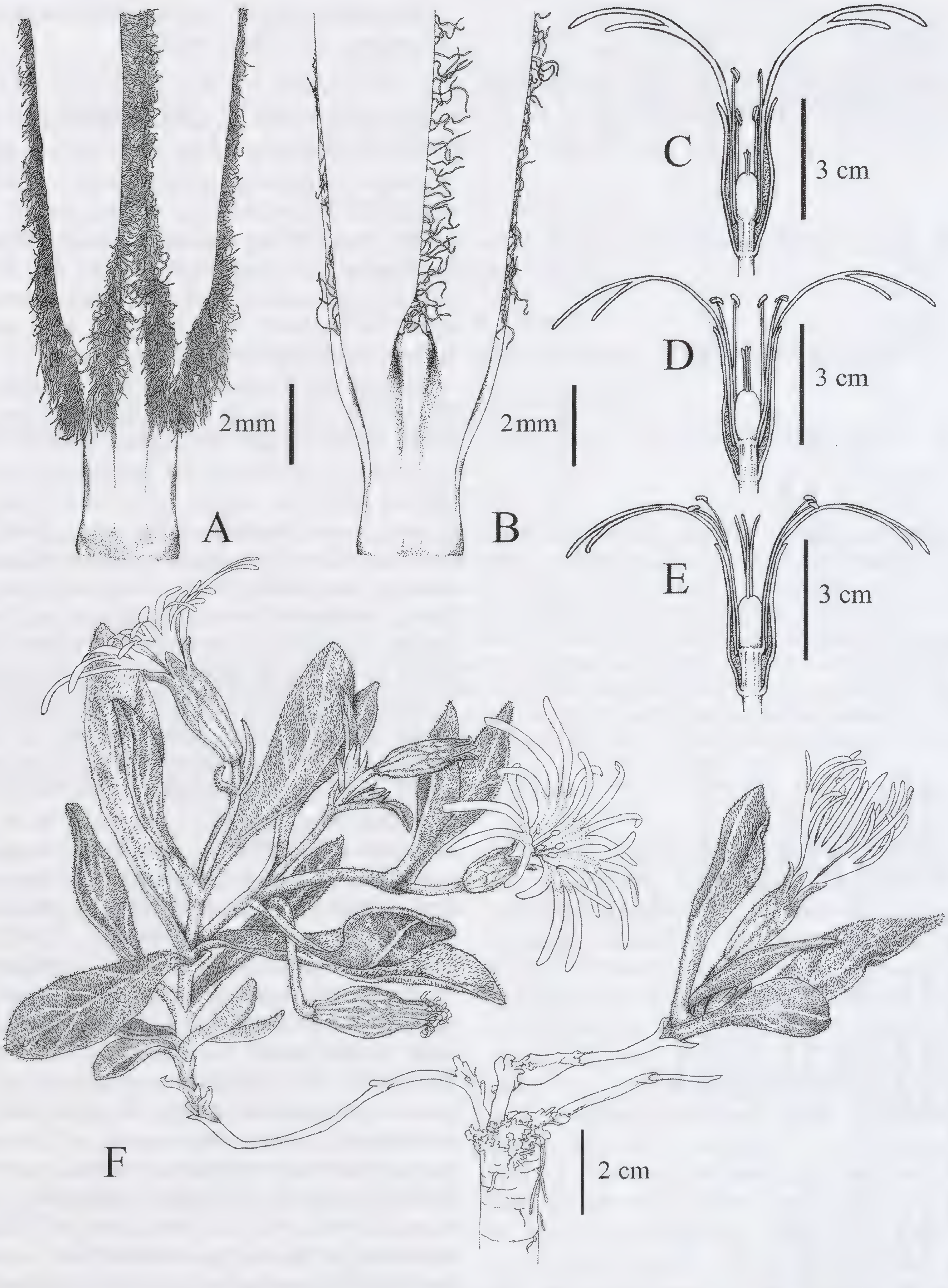

FIG. 1. Morphological features of *S. nelsonii* and *S. bolanderi*. *S. nelsonii* (A, C–F). *S. bolanderi* (B). A–B. Flower dissections showing anthophore, petal bases, and antisepalous filament base (partially obscured by hairs in A). C–E. Change in corolla shape in transition from male to female stages. F. Habit. Note post-anthesis flower with enlarged calyx at the tip of deflexed pedicel.

flabelliform, deeply 4-(6)-lobed, lobes of adjacent petals often overlapping; lobes usually extending to base of claw, narrow, linear to tapering from base or narrowly oblanceolate, 8.7–31.5 mm long, 1.0–3.0 mm wide (length:width ratio [3.5] 6–20.0), outer lobes +/- equal to inner lobes or shorter (inner:outer ratio 0.67–0.99), tips blunt to rounded to acute, sometimes notched; stamens in two sets of 5, shorter than or +/- equal to claw, filaments radially arranged, white, initially erect as anthers dehisce, elongating and recurving onto petals [female phase], 12–22 mm; anthers white, initially erect, becoming perpendicular to filament, members of each set dehiscing +/- synchronously; styles 3, initially shorter than stamens and appressed [male phase], elongating and spreading with age, not strongly exserted when mature, curved at tip, 11–19 mm; ovary cylindrical to narrowly obpyriform, 4–5 mm long, 1.7–2.7 mm wide; capsule ovoid to globose, enclosed by persistent calyx, stalked, +/- erect when maturing (via sharp bend at tip of pedicel), positioned at or near ground level at maturity, opening by 6 short, +/- recurved

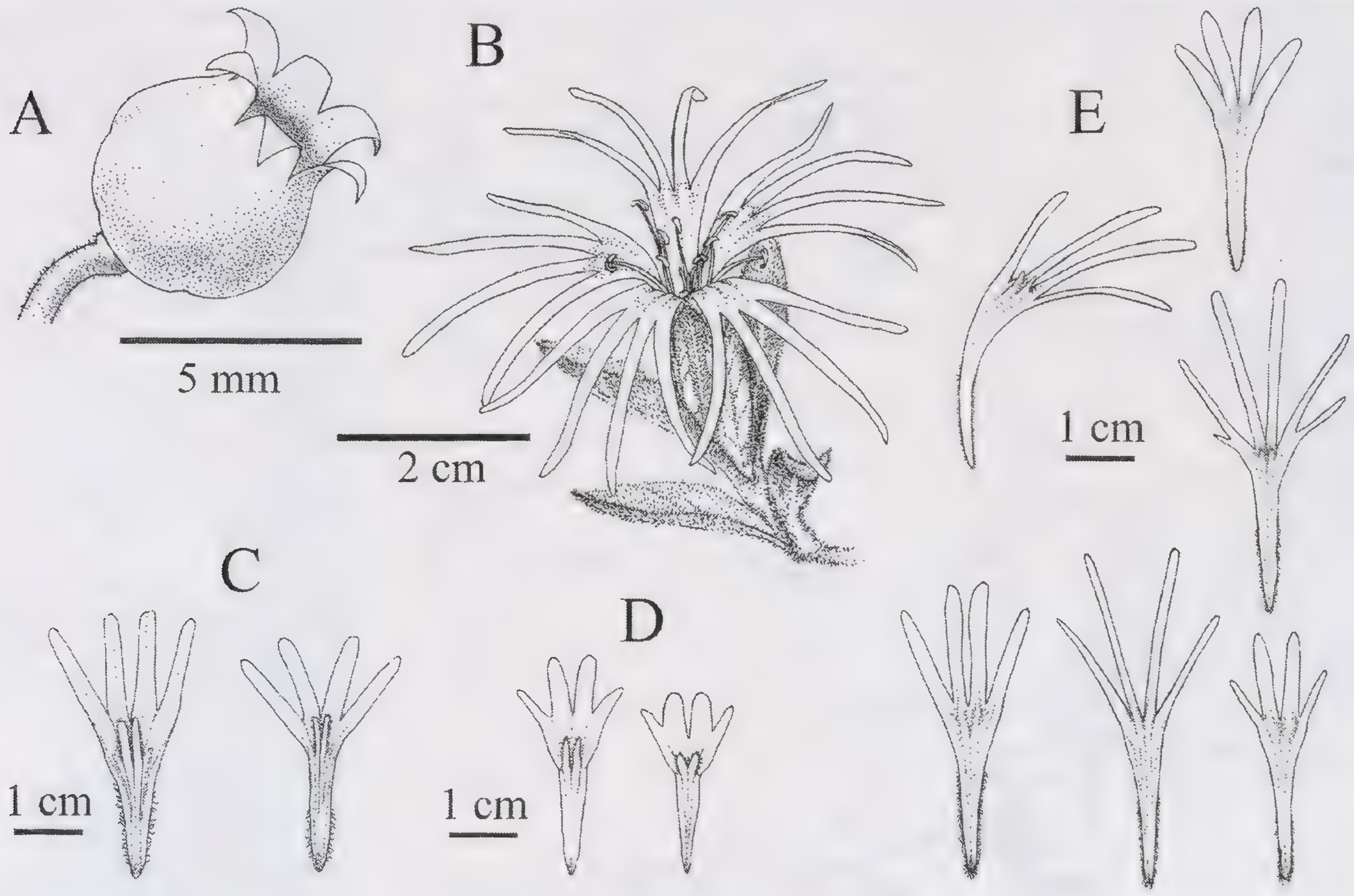

FIG. 2. Morphological features of *Silene nelsonii*, *S. bolanderi*, and *S. hookeri*. *S. nelsonii* (A, B, E). *S. bolanderi* (C). *S. hookeri* (D). A. Mature fruit. B. Male phase flower. C–E. Variation in petal lobing within and among species.

teeth, 6–10 mm long, 5.5–7.3 mm wide; seeds dark reddish brown, papillate, 2.0–2.25 mm long, 1.75–1.25 mm wide.

Paratypes (arranged alphabetically by collector within county. Note: locality information, including spatial coordinates (NAD 27), is provided only when given on the collection label. USA, California, **Humboldt County**: Brush Mountain, 26 May 1983, *Jimerson sn* (CAS); FS 5N40 about 3.2 miles from NF 60, 45°66′48″E, 45°12′644″N, 4092 ft, 3 Jun 2013, *Mesler 1481* (HSC); FS 6, 1 mile south of Sims Mtn, 44°91′17″E, 45°08′191″N, 3600 ft, 5 May 2018, *Mesler 1665a* (HSC); FS 6 near Manzanita Ranch, 45°39′45″E, 45°07′575″N, 1680 ft, 19 May 2018, *Mesler 1667* (HSC); Friday Ridge Road, near intersection with Hwy 299, 7 May 1978, *Reed 45* (HSC); Brannan Mountain, 7 July 1911, *Tracy 3414* (UC); **Trinity County**: Burnt Ranch USFS campground, 412 m, 30 April 1983, *Janeway 245* (HSC); Weaverville, *Kleeberger sn* (CAS); Hyampom Rd, west of Hayfork, 47°88′46″E, 44°91′662″N, 2100 ft, 7 June 2011, *Mesler* (HSC); Wildwood Rd, near Gemmill Gulch, 49°52′14 E 44°75′752 N, 3290 ft, 30 May 2010, *Mesler 818* (HSC); Weaverville, Garden Gulch Trail, 50°43′99 ″E, 45°11′070″N, 2300 ft, 7 June 2010, *Mesler 821* (HSC); North of Hyampom along NF 60, 47°84′92″E, 44°91′919″N, 2300 ft, 29 May 2011, *Mesler 846* (HSC); south of Indian Valley Guard Station along NF 7, 47°53′73″E, 44°79′258″N, 4000 ft, 8 Jun 2011, *Mesler 852* (HSC); North of Indian Valley Guard Station on NF 10, 47°06′14″E, 44°87′503″N, 4050 ft, 8 Jun 2011, *Mesler 853* (HSC); Philpot Camp near Peanut, 48°39′61″E, 44°79′171″N, 2600 ft, 26 May 2013, *Mesler 1479* (HSC); FS 30°N01 near Wildwood, 50°00′28″E, 44°71′971″N, 4380 ft, 26 May 2013, *Mesler 1480* (HSC); Ewing Reservoir, Hayfork, 2440 ft, 48′5817 E, 49°90′223″N, 2440 ft, 20 May 2018, *Mesler 1671* (HSC); south of Wildwood on FS 29N28, 49°41′19″E, 44°67′765″N, 27 Jun 2018, 4100 ft, *Mesler 1690* (HSC); FS 60 6.6 mi south of Hwy 299, 45°93′73″E, 45°13′111″N, 3500 ft, 30 May 1980, *Nelson 5347* (HSC67250); FS 60 10 mi south of Hwy 299, 4400 ft, 30 May 1980, *Nelson 5360* (HSC); 2 miles east of Burnt Ranch, 16 Jun 1964, *Spellenberg 438* (HSC); east side of Underwood Mtn Rd (5N09), ca. 4.9 miles south of Hwy 299, 12-June-1980, *Taylor 2855* (CHSC); near summit of Hayfork Mountain on Weaverville Rd 30 June 1923, *Tracy 6444* (UC); Burnt Ranch, 1500 ft, 27 April 1924, *Tracy 6655* (UC275265); north of Philpot campground, 2600 ft, 13 May 1979, *York 286* (HSC); **Shasta County**: Basin Gulch Camp, 50°33′55″E, 44°66′872″N, 2570 ft, 4 May 2013, *Mesler 1476* (HSC).

DISTRIBUTION AND HABITAT

Silene nelsonii is restricted almost entirely to Trinity County in an area bounded by the Main Stem and South Fork of the Trinity River. Exceptions are three sites due west of the Main Stem and another location between the South and Stuart Forks of the river (Figs. 3, 4). Plants generally grow in deep, well-drained soils in grassy openings near ephemeral drainages and along roads in cismontane woodland or lower montane coniferous forest at elevations of 85 to 1400 meters. Substrates are generally either ultramafic or metasediments. Common associates are *Ceanothus cuneatus* (Hook.) Nutt., *Festuca californica* Vasey, *Pinus jeffreyi* Grev. & Balf. *in* A. Murray, *P. ponderosa* Dougl. ex P. & C. Lawson, *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus garryana* Dougl. and *Q. kelloggii* Newb.

PHENOLOGY

Silene nelsonii flowers from mid-April to June; fruits begin to mature by late June.

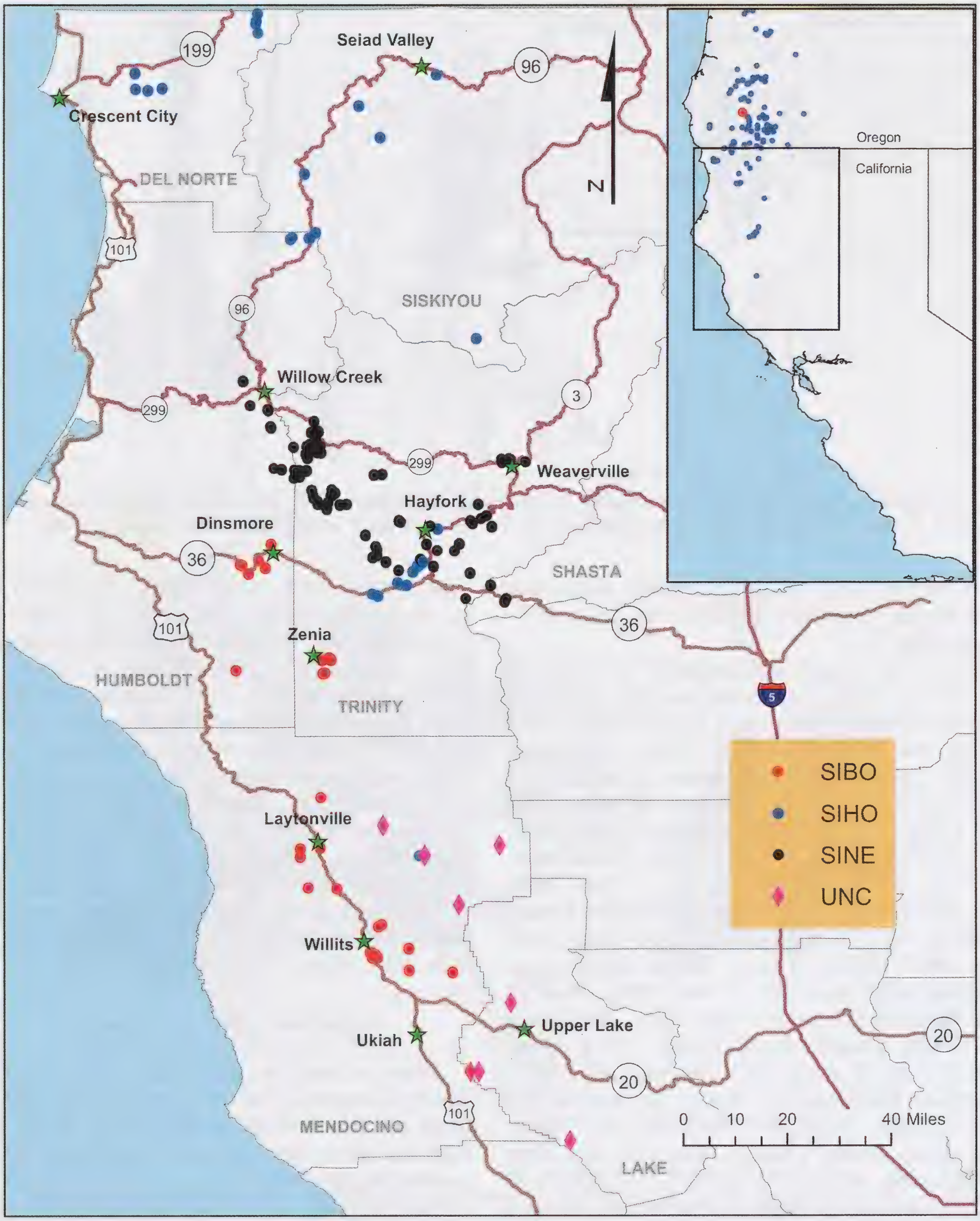

FIG. 3. Distribution of the *Silene bolanderi*, *S. hookeri*, and *S. nelsonii* in northwestern California. Inset shows full range of *S. hookeri* and the location of the Wolf Creek population in Josephine County, Oregon (red dot). SIBO = *S. bolanderi*; SIHO = *S. hookeri*; SINE = *S. nelsonii*; UNC = populations in Lake and Mendocino counties that could not be identified with certainty. Plotted occurrences based on herbarium records and recent observation.

ETYMOLOGY

The specific epithet *nelsonii* honors the late Thomas W. Nelson (1928–2006), who first drew our attention to the beautiful plants near Burnt Ranch. He was an avid student of the flora of northwestern California (Collections Manager, HSC, c. 1975–1985) and the first author of two species in the *Silene hookeri* complex (*S. salmonacea* T.W.Nelson, J.P.Nelson & S.A.Erwin and *S. serpentinicola* T.W.Nelson & J.P.Nelson).

Suggested common name: Nelson's Stringflower.

MATERIALS AND METHODS

Description of the new species was based on examination of fresh material collected from most of the known occurrences, as well as specimens from the

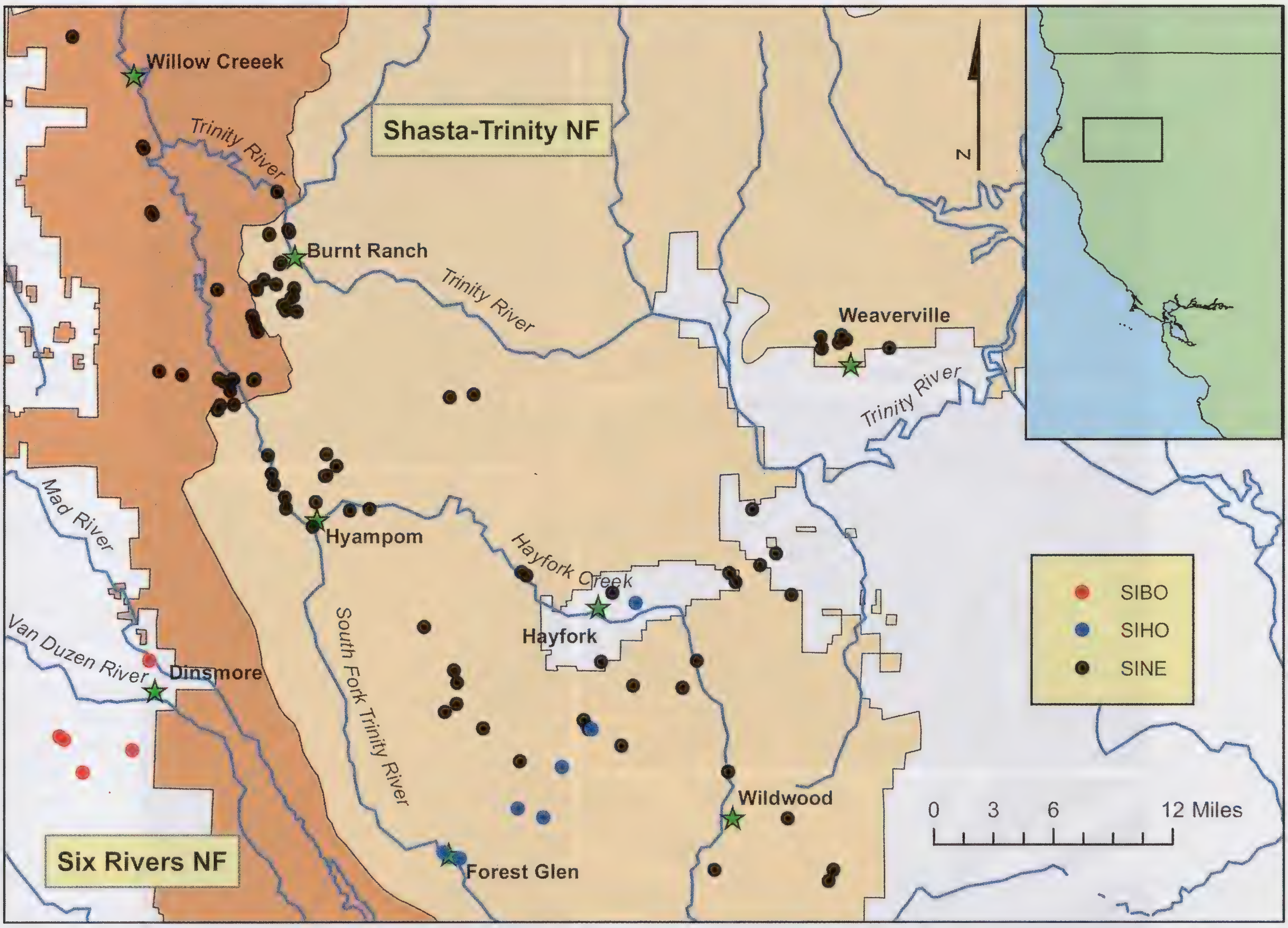

FIG. 4. Distribution of *S. nelsonii*. SIBO = *S. bolanderi*; SIHO = *S. hookeri*; SINE = *S. nelsonii*. All but two of the SINE occurrences confirmed extant by recent field work.

following herbaria: HSC, CAS, DS, JEPS, and UC. We also examined herbarium specimens, including online images of types (via JSTOR Global Plants), and fresh material from northwestern California and western Oregon representing the other elements of the *Silene hookeri* complex, here provisionally construed to include *S. bolanderi*, *S. hookeri*, *S. nelsonii*, *S. serpentinicola*, and *S. salmonacea* based on morphological similarity (Appendix 1). We treat *S. serpentinicola* as a distinct species (Nelson and Nelson 2004) – not as a subspecies of *S. hookeri* as proposed by Chambers and Meyers (2011) – based on newly discovered morphological differences between the two taxa (Mesler, unpublished data).

We could not locate the type locality of *S. bolanderi* ("Long Valley"), which presumably lies somewhere between Laytonville and Longvale (Mendocino County), but were able to study a few populations that match Gray's concept of the species (and key to *S. hookeri* subsp. *bolanderi* in Hitchcock and Maguire 1947): Zenia Guard Station (Humboldt Co: *Mesler 1195*, HSC), Dyerville Loop (Humboldt Co: *Mesler 1649*, HSC); Tomki Road (Mendocino Co: *Mesler 1187*, HSC), and Wolf Creek (Josephine Co: *Mesler 1183*, HSC). The Wolf Creek population is one of approximately 20 reported from Josephine County in Oregon (S. Vrilakas, Oregon Biodiversity Information Center, personal communication). Many historical occurrences of this taxon in California are apparently either extinct or located on inaccessible private property. Only two small populations of *S. hookeri* subsp. *pulverulenta* (M.Peck) C.L.Hitchc. & Maguire could be studied in the field (Jackson Co., Oregon: *Mesler 1180*, *1181*, HSC), so description of *S. hookeri* is based on plants assignable to *S. hookeri* subsp. *hookeri* from Humboldt, Siskiyou, and Trinity counties in California, and Josephine and Douglas counties in Oregon per Hitchcock and Maguire (1947). Two confusing populations in Mendocino County that appeared intermediate between *S. bolanderi* and *S. hookeri* were also studied: Poonkinney Road (*Wayman 283*, HSC) and Rickabaugh Glade (*Mesler 1185*, HSC). For completeness, we include all five species in our key, but our morphological analysis focuses on comparisons of *S. bolanderi*, *S. hookeri*, and *S. nelsonii* because of the historical confusion about the boundaries of these taxa.

Examination of fresh flowers was critical because several important characters, such as the three-dimensional shape and diameter of the corolla, petal color, the presence/absence of coronal appendages, and the symmetry and pattern of maturation of the androecium, can be difficult or impossible to assess

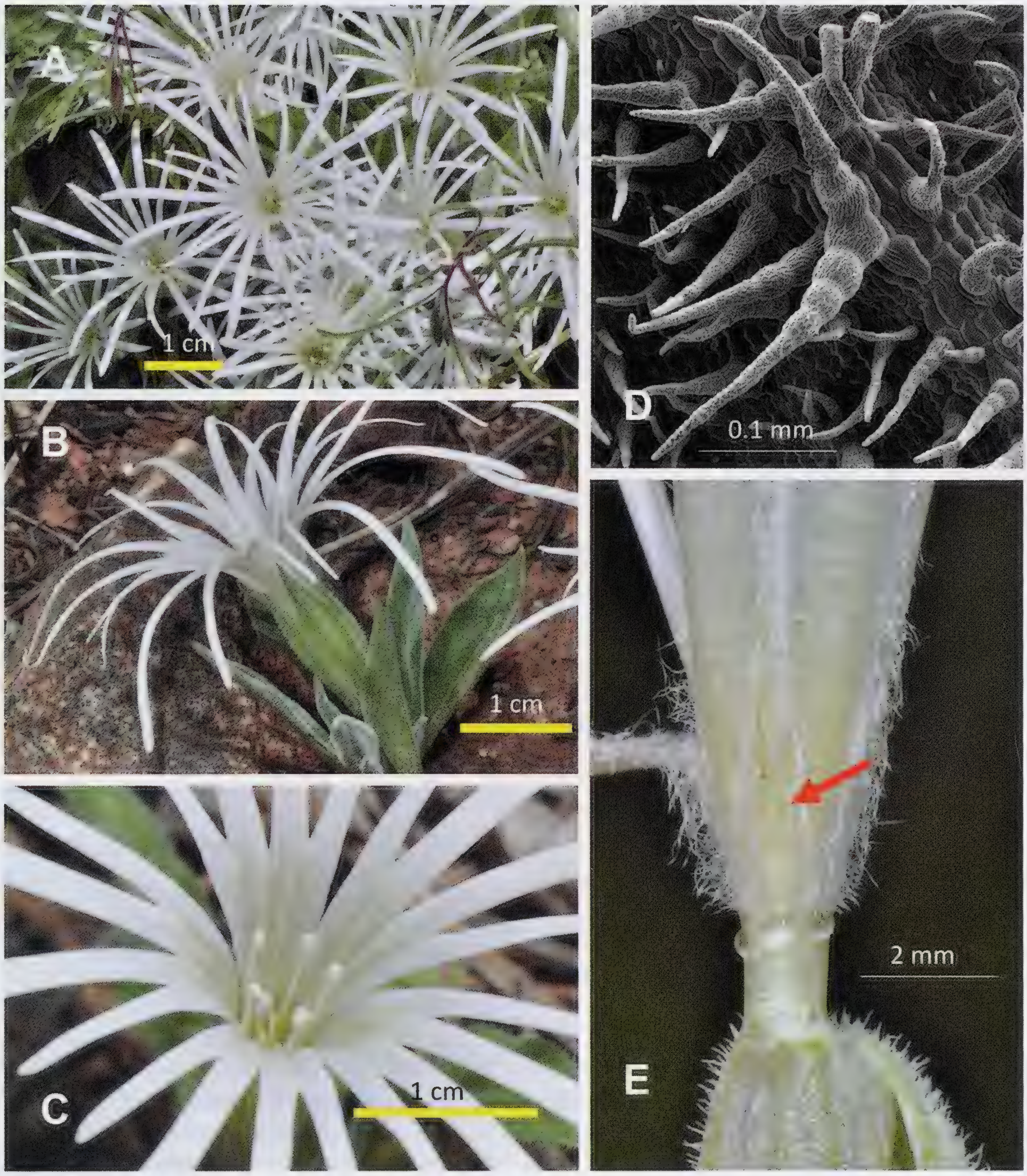

FIG. 5. *Silene nelsonii.* A. Philpot Campground, Trinity County, CA. B–D. Near Underwood Mountain, Humboldt County, CA. A. Individual petals difficult to discern because outer lobes of adjacent petals overlap. B. Flower larger than the vegetative body of the plant; note funnelform corolla. C. Inner antisepalous stamens with dehisced anthers; note radial symmetry. D. Sepal hairs. E. Calyx dissected to show anthophore with nectar droplets; bases of two petals outlined by dense cilia. Nectar window and filament base (red arrow) obscured by petal hairs.

using dried material. Flower measurements were made using digital calipers, a dissecting microscope fitted with an ocular micrometer, or the computer program ImageJ (Rasband, 1997–2018). Petals were conveniently studied by flattening them on card stock, sprayed first with artist's adhesive, and then photographing with a ruler scale. The following measurements were taken for each petal: total length (measured from the base to the arc connecting the tips of the inner lobes); limb length (measured from the base of the coronal appendages); central sinus depth (measured from the sinus between the two inner lobes to the arc connecting the tips of the inner lobes); inner and outer lobe length (both measured from the level of one of the outer sinuses to the tip); inner and outer lobe width (both measured at the level of one of the outer sinuses); and appendage length (measured as the part free from the petal surface). Additional traits were calculated as ratios based on these measurements (Table 2). Specimen sampling was not random, but instead focused on characterizing the range of trait values. Thus we do not report means, standard deviations, or statistical comparisons. Although generally reserved for sympetalous flowers, we use the terms salverform and funnelform because they aptly describe an important difference in overall corolla shape. We follow Jurgens (2006) in using the term anthophore (vs. carpophore) for the stalk-like structure that elevates the ovary above the calyx because it corresponds to the bases of the corolla, androecium, and gynoecium.

Table 2. Floral Traits Useful for Distinguishing *Silene bolanderi*, *S. hookeri*, and *S. nelsonii*. Trait value ranges for the Poonkinney Road and Rickabaugh Glade populations are given, in that order, in brackets. See "Methods" for an explanation of petal measures.

	S. bolanderi	*S. hookeri*	*S. nelsonii*
Corolla shape (male phase)	narrowly to broadly funnelform, petal limbs ascending to recurved	salverform, petals limbs +/- perpendicular to claws	narrowly to broadly funnelform, petal limbs ascending to recurved
Corolla throat (male phase)	+/- broadly open; exposed upper petal claws white to pink, paired ridges prominent	narrow; exposed upper claws white to pink, paired ridges prominent	broadly open; exposed upper claws translucent gray, paired ridges gen weak
Corolla diameter (mm)	27–58 [33–42; 24–43]	21–40	16–75
Corona appendages	linear, >1 mm	linear, >1 mm	absent or inconspicuous short teeth, gen <1 mm
Petal length (mm)	29–42 [28–37; 25–30]	23–32	20–56
Petal limb color	pale pink (rarely white)	pale to deep pink (rarely white)	white
Petal limb length (mm)	14–23 [13–20; 12–17]	6–17	9–33
Central sinus depth: limb length ratio	0.6–0.9 [0.5–0.7; 0.6–0.7]	0.3–0.9	1
Inner lobe length (mm)	9–17 [4–10; 4–7]	2–10	8–32
Outer lobe length (mm)	8–15 [4–10; 4 – 7]	1–7	6–26
Inner lobe shape (length:width ratio)	narrowly oblong to linear, 4–8 [2–4; 2–4]	oblong, 1–5	linear, 6–24
Outer lobe shape (length:width ratio)	3 – 9 [2–6; 2–5]	1–6	4–17
Outer vs. inner lobe length ratio	0.6–1.0 [0.5–0.9; 0.6–1.0]	0.4–1.0	0.6–0.9
Outer vs. inner lobe width ratio	0.6–1.1 [0.5–0.9; 0.6–1.0]	0.3–0.9	0.7–1.6
Petal base margin, visibility of antisepalous filaments	glabrous, filaments clearly visible	glabrous, filaments clearly visible	sparsely to densely ciliate, filaments at least partially obscured by hairs
Androecium symmetry, within-whorl anther dehiscence	+/- radial, anther dehiscence +/- synchronous	+/- bilateral, asynchronous	+/- radial, anther dehiscence +/- synchronous
Calyx hairs	simple, long, slender, curled at tip, glandular or not	simple or rarely branched at base, long, slender, curled at tip, glandular or not	simple or branched at base, relatively short, not curled, not glandular

Twenty-seven populations were chosen to represent the geographic range and taxonomic diversity of the *S. hookeri* complex in the analysis of DNA sequence variation (Appendix 2). All but the Eden Valley population in Mendocino County (*Nelson 9118*) were studied in the field. *Silene laciniata* Cav. and *S. menziesii* Hook. serve as outgroups because they are, respectively, representatives of the tetraploid and diploid lineages that likely gave rise to allohexaploid *S. hookeri* (Popp and Oxelman 2007). However, because ITS vs. cpDNA topologies differ for *Silene* (Popp and Oxelman 2007), we used *S. laciniata* and *S. menziesii* to root the ITS tree, but just *S. laciniata* to root the cpDNA tree. One dried field-collected specimen per population provided tissue for total DNA extraction (Pepper and Norwood 2001) and PCR amplification. Four regions (*trnH – psbA*, *trnQ – 5′rps16*, *rpL16*, *rpS16*) in the chloroplast genome (cpDNA) were targeted because they have exhibited variation among closely related species across a wide sampling of spermatophyte taxa (Shaw et al. 2005, 2007, including PCR primers and protocols). The internal transcribed spacer region (ITS-1, the 5.8s ribosomal RNA gene, and ITS-2) supplied an independent set of sequence data for a subset (21 of 32) of the specimens in the cpDNA data set. Primers (P17 and 26S-82R) and protocol for amplification of ITS followed Popp and Oxelman (2001, 2007), except that we lowered the annealing temperature to 54–56°C.

Sequencing of purified PCR products utilized the same primers as PCR, and was carried out by Retrogen, Inc. (San Diego, CA). Alignment of resulting sequences (See Appendix 2 for Genbank accession numbers) was done by eye; gaps were coded as missing data but indels were coded as additional binary characters following a simple indel coding strategy (Simmons and Ochoterena 2000). Highly variable microsatellite loci within these regions were excluded from the analysis. The four cpDNA regions were analyzed as a single data set, separate from the ITS data.

Phylogeny estimation employed Maximum Parsimony (PAUP* version 4.0a build 162; Swofford, 2002) and Bayesian analyses (MrBayes v. 3.2.2; Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003). The parsimony analysis included 10 replicate heuristic searches with random addition of taxa, tree bisection-reconnection (TBR) branch-swapping, option DELTRAN, and equal-weighted characters. Bootstrap analysis of 1000 replicates using the "fast" option in PAUP* was used to examine support for the clades. We used jModelTest 2.1.10 (Darriba et al. 2012) to identify the appropriate evolutionary models for the Bayesian analyses: HKY + I + G for the cpDNA segments, K80 for the ITS region. Analyses included one-million generations with four chains, sampling trees every 100 generations; a majority-rule consensus tree with posterior probabilities was constructed after a 25% burn-in.

RESULTS

Morphological Comparisons

Silene bolanderi, *S. hookeri*, and *S. nelsonii* resemble one another in several respects, both vegetatively and reproductively. In all three species, one to often several slender, shallowly buried rhizomes radiate from the crown of a deep tap root, and ultimately emerge as a cluster of simple or sparingly branched, decumbent to erect, aerial shoots (Fig. 1F). Each aerial shoot typically bears ≤ 3 closely spaced pairs of elliptical to narrowly oblanceolate leaves and one or a few showy flowers in a terminal dichasium. Stems and leaves are sparsely to densely canescent and green to gray-white. Except in relatively mesic sites, where internodes are longer, aerial shoots are often short (<10 cm) and flowers borne near ground level. Flowers of the three species are large (generally ≥ 2.5 cm across), upright or ascending, non-fragrant, day-blooming, and protandrous. Petals are differentiated into a narrow, +/- translucent claw and a greatly expanded, four-lobed limb. The margins of the claws overlap for most of their length forming a tube except at the very base, where five +/- elliptical gaps ("nectar windows") provide access for pollinator proboscides to reach droplets of nectar that accumulate on the surface of the anthophore. The base of one of the five antisepalous filaments bisects each gap (Figs. 1A, B, 5E, 6E). Two parallel ridges run up from about the distal one-third of the claw to the intersection with the limb. When present, coronal appendages emerge as extensions of these ridges. The androecium consists of two sets of five stamens, the antisepalous maturing before the antipetalous. After pollination, pedicels elongate and bend sharply downward, bringing mature capsules to (or close to) ground level (Fig. 1F). Capsules are globose with an apical pore surrounded by six short recurved teeth (Fig. 2A).

Silene bolanderi and *S. nelsonii* share several floral features that set them apart from *S. hookeri* (Table 2). Both species have larger (diameter usually >3.5 cm), relatively open, deeply lobed flowers (ratio of central sinus depth:limb length at least 0.6). Petal lobes are usually long and slender (length:width ratio typically ≥ 5); inner lobes and outer lobes are approximately equal in size, although the outer lobes are usually at least slightly shorter and narrower at the base (Figs. 2B, C, E). As flowers of both species open and anthers begin to dehisce, the petal claws stand close together and +/- parallel inside the calyx, and petal limbs are oriented at approximately 45° to the claws (Fig. 1C), forming a narrow throat. But both claws and limbs diverge by the time styles begin to elongate, and petal lobes gradually arch and often recurve, resulting in a more open, narrowly to broadly funnelform corolla with a poorly defined broad throat, and exposing the upper surface of the claw (Figs. 1E, 2B, 5C, 6A, B, C). The androecium of both species is radially symmetrical, with stamens erect and +/- evenly spaced around the perimeter of the throat (Figs. 5C, 6C). Anthers in each set dehisce +/- synchronously. After dehiscence, filaments elongate and recurve onto the surface of the petals (Figs. 1E, 2B). In contrast, the flowers of *S. hookeri* are generally smaller (diameter usually ≤ 3 cm), and petals more shallowly and more unequally lobed (Table 2; Figs. 2D, 7A). Inner lobes are generally oblong, and outer lobes narrowly lanceolate or sometimes tooth-like (Figs. 2D, 7A). Like most other *Silene*, the petals of *S. hookeri* are bent at a +/- 90° angle at the intersection of limb and claw, forming a salverform corolla with a narrow, well-defined throat (Figs. 7A, B). Although stamens arise from the anthophore in radial fashion, some of the filaments tilt such that most or all of the anthers are positioned on one side of the corolla throat (Fig. 7B). Anthers within a set do not dehisce synchronously; typically, two of the five antisepalous stamens open first, soon followed in sequential fashion by the remaining antisepalous stamens and then by the antipetalous stamens.

The obvious differences between *S. hookeri* and *S. nelsonii* are consistent, but the distinction between *S. bolanderi* and *S. hookeri* appears to break down at two sites in Mendocino County (Table 2). The flowers of plants at Rickabaugh Glade fall into the range of *S. hookeri* in terms of petal color (dark pink), size, depth of petal lobing, and lobe shape, but overall corolla shape (relatively open with flaring petal limbs) and androecium symmetry are consistent with *S. bolanderi*. Flowers at the Poonkinney Road site are pale pink, relatively large and open, but petal limbs are more shallowly and unequally lobed than most *S. bolanderi*. Androecium symmetry at this site varies among individuals from +/- radial to bilateral. Based on examination of a limited number of difficult-to-interpret herbarium specimens, a few additional populations in eastern Mendocino and adjacent Lake counties (Fig. 3) may likewise prove

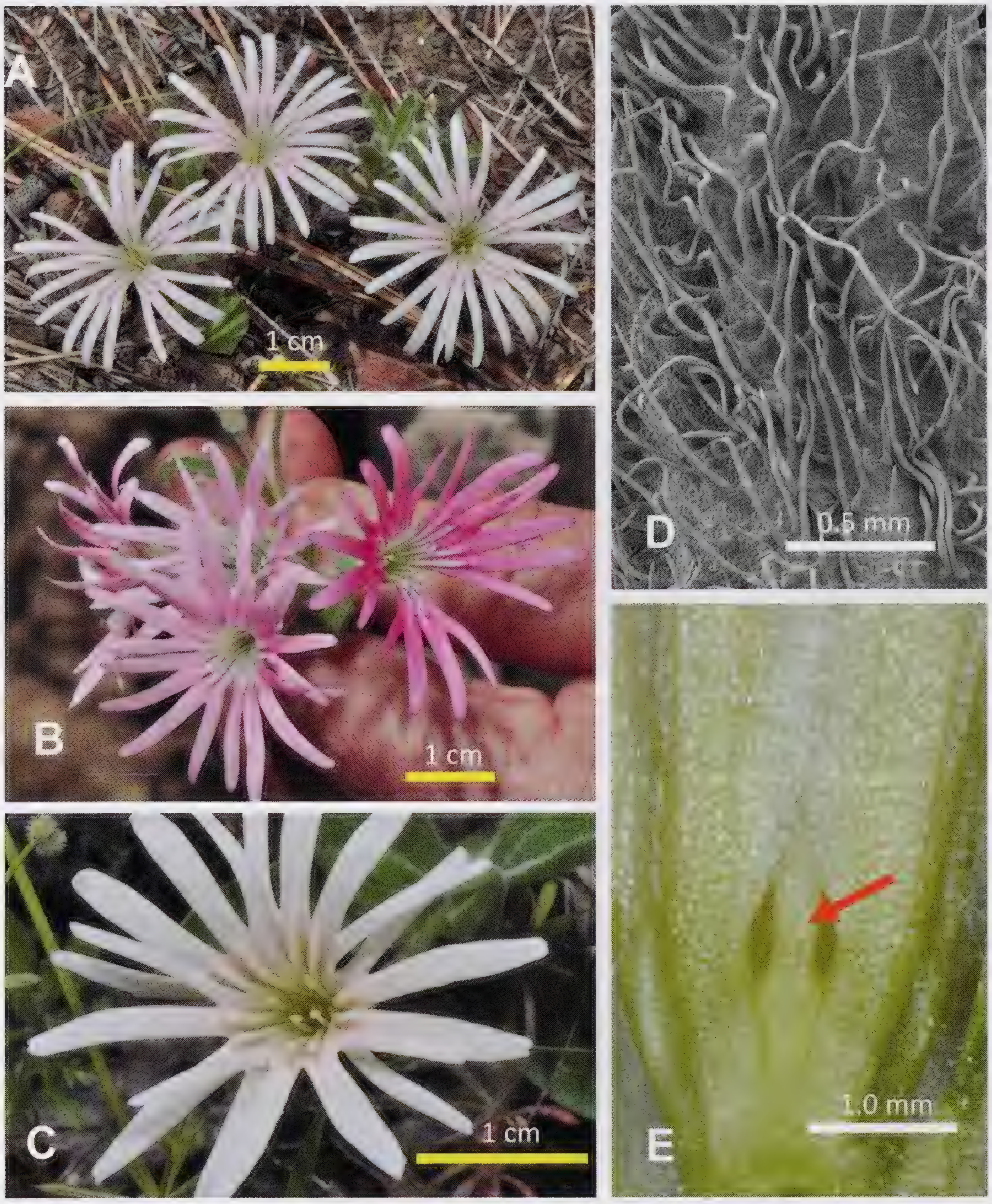

FIG. 6. *Silene bolanderi*. A. Zenia, Trinity County, CA. B. Tomki Road, Mendocino County, CA. C. Dyerville Loop Road, Humboldt County. A–C. Male phase flowers. Note radially arranged antisepalous stamens with dehisced anthers and prominent coronal petal appendages in C. D. Sepals hairs. E. Calyx dissected to show anthophore; glabrous bases of two petals flank nectar window with clearly visible filament base (red arrow).

difficult to assign unambiguously to *S. bolanderi* or *S. hookeri* if eventually seen again in the field. This impression is supported by label annotations for two of these specimens, both identified as *S. hookeri* subsp. *bolanderi*. LeRoy Abrams annotated *Bacigalupi 1526* (DS159849) as "intermediate between typical *hookeri* and subsp. *Bolanderi*," and the collectors of *Hamann and Dearing 1113A* (JEPS) noted that "this ssp. is very variable as to its principle and purportedly diagnostic features." The set of problematic specimens includes a collection from Eden Valley (*Nelson 9118*, HSC) that was included in the phylogenetic analysis.

Silene nelsonii can be distinguished from *S. bolanderi* most easily and reliably by differences in petal color, depth of petal lobing, expression of petal appendages, and vestiture at the base of petals (Table 2). The petal limb of *S. nelsonii* is consistently white; petal limb color in *S. bolanderi* is pale pink (Figs. 5, 6), although occasional white-flowered plants occur in some populations. Petals typically spread broadly in *S. nelsonii*, creating a broadly open flower center, which is pale translucent gray (sometimes with a faint green cast caused by reflections from the ovary and calyx, not pigmentation) (Fig. 5A, C). In contrast, the flower center of *S. bolanderi* is somewhat less open and white or pink (Fig. 6A–C). The petals *of S. nelsonii* are lobed to the base of the limb compared to generally less than 0.7 of the distance to the base in *S. bolanderi* (Figs. 2C, E, 6A–C). Like *S. hookeri*, the petals of *S. bolanderi* have well-developed coronal appendages at the intersection of claw and limb. These appear as extensions of the paired claw ridges, which are prominent and thick in this species (Figs. 2C, 6A–C). In contrast, the claw ridges of *S. nelsonii* are usually less robust, and most often end just proximal to the base of the inner petal lobes (Figs. 2E, 5C). In some cases, however, the ridges are more

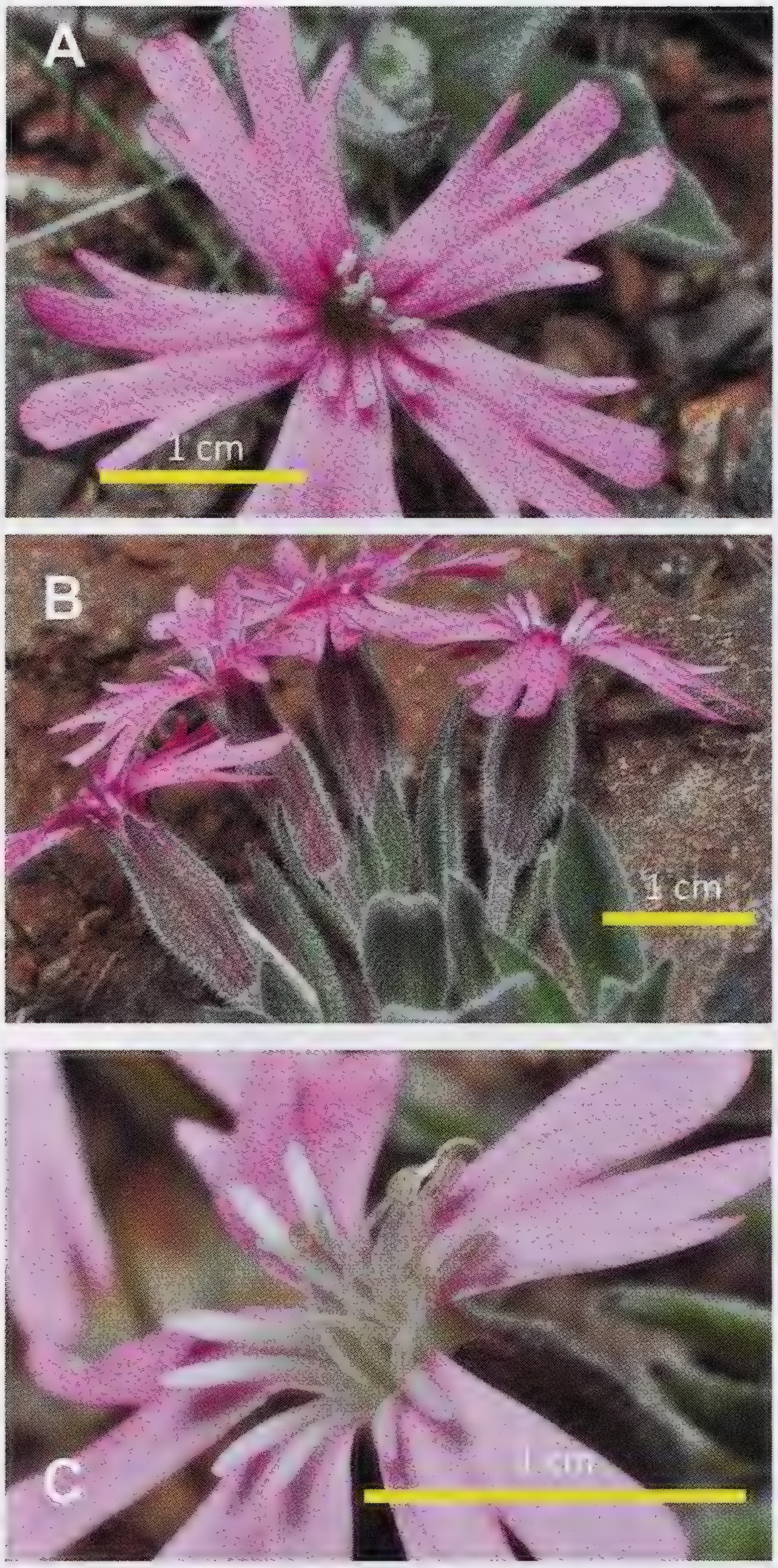

FIG. 7. *Silene hookeri*. A, B. French Hill Road. C. Philpot Campground, Trinity County. A. Petal limbs unequally and shallowly lobed; note position of anthers on one side of the throat. B. Bend at the juncture of limb and claw creates a salverform corolla. C. Female stage flower; note position of filaments on upper side of the throat.

robust and extend as short, rudimentary teeth. Petals of S. *nelsonii* are usually densely woolly ciliate at the base, and hairs cover the nectar window and underlying filaments (Figs. 1A, 5E). In contrast, the petal bases of *S. bolanderi* (and *S. hookeri*) are generally glabrous below the top of the nectar window and filament bases are clearly visible with a hand lens (Figs. 1B, 6E). Sepal hairs of *S. nelsonii* are non-glandular and typically relatively short and tapered from a broad base. In contrast, sepal vestiture in *S. bolanderi* varies from glandular to non-glandular within and among populations; non-glandular hairs are long, slender, curled at the tip, and unbranched (Figs. 5D, 6D). Flowers of *S. nelsonii* also tend to be larger with longer, narrower, and more strongly recurved petal lobes, but there is overlap for all of these traits (Table 2).

Molecular Phylogenetic Analysis

The concatenated alignment of non-coding cpDNA sequences generated in the present study consisted of *trnH – psbA* (312 bases, 11 indels), *trnQ – 5′rps16* (756 bases, 8 indels), *rpL16* (929 bases, 12 indels), and *rpS16* (891 bases, 12 indels). The ITS sequence alignment comprised 632 bases, with no indels. Strict consensus trees summarizing the results of the Maximum Parsimony and Bayesian analyses exhibited congruent topologies for the cp data, and likewise for the ITS data, thereby allowing reporting of the results using just two trees (Fig. 8). The clade of *Silene nelsonii* exemplars is recovered with 100% posterior probability and bootstrap confidence in both trees, sister to *S. menziesii* in the cp tree and to the clade of *S. bolanderi* + *S. hookeri* in the ITS tree. The contrasting position of *S. menziesii* in the two trees was unexpected, and was not influenced by outgroup choice. Morphologically unambiguous representatives of *S. bolanderi* form a strongly-supported clade in both trees with the exception of the plant sampled from Wolf Creek (Josephine County, Oregon), which shared no synapomorphies with the other *S. bolanderi* samples in the ITS tree. The morphologically ambiguous individual from Rickabaugh Glade nested as part of the *S. bolanderi* clade on both trees. In contrast, the representative from Poonkinney Road was nested within the *S. bolanderi* ITS clade, but sister to the entire *S. bolanderi* + *S. hookeri* clade in the cp tree. Finally, both cp and ITS topologies depict *S. hookeri* as non-monophyletic, regardless of the analytical approach.

DISCUSSION

Silene nelsonii is arguably one of the most distinctive North American members of the genus. We base our decision to recognize it as a separate species on morphological differences, strong support from the molecular analysis, and almost complete geographical separation – evidence which, taken together, indicates an evolutionarily independent lineage. Earlier workers likely missed the obvious morphological distinction between *S. nelsonii* and *S. bolanderi* because they did not see *S. nelsonii* in the field owing to its restricted geographical distribution and because of the limited number of herbarium collections available for examination. A review of online databases and herbarium loans revealed only 15 collections assignable to *S. nelsonii* by 1947, when Hitchcock and Maguire published their revision of North American *Silene*. These authors examined two of the 15, both annotated as *S. hookeri* subsp. *bolanderi* (*Abrams 7114*, DS; *Tracy 6655*, UC). Only 65 collections were available by the time the *Flora North America* treatment of *Silene* was published (Morton 2005), 60% of which were held at HSC, hundreds of miles from major herbaria. Adding to the difficulty, even well-prepared pressed specimens of *S. nelsonii* and *S. bolanderi* can be difficult to

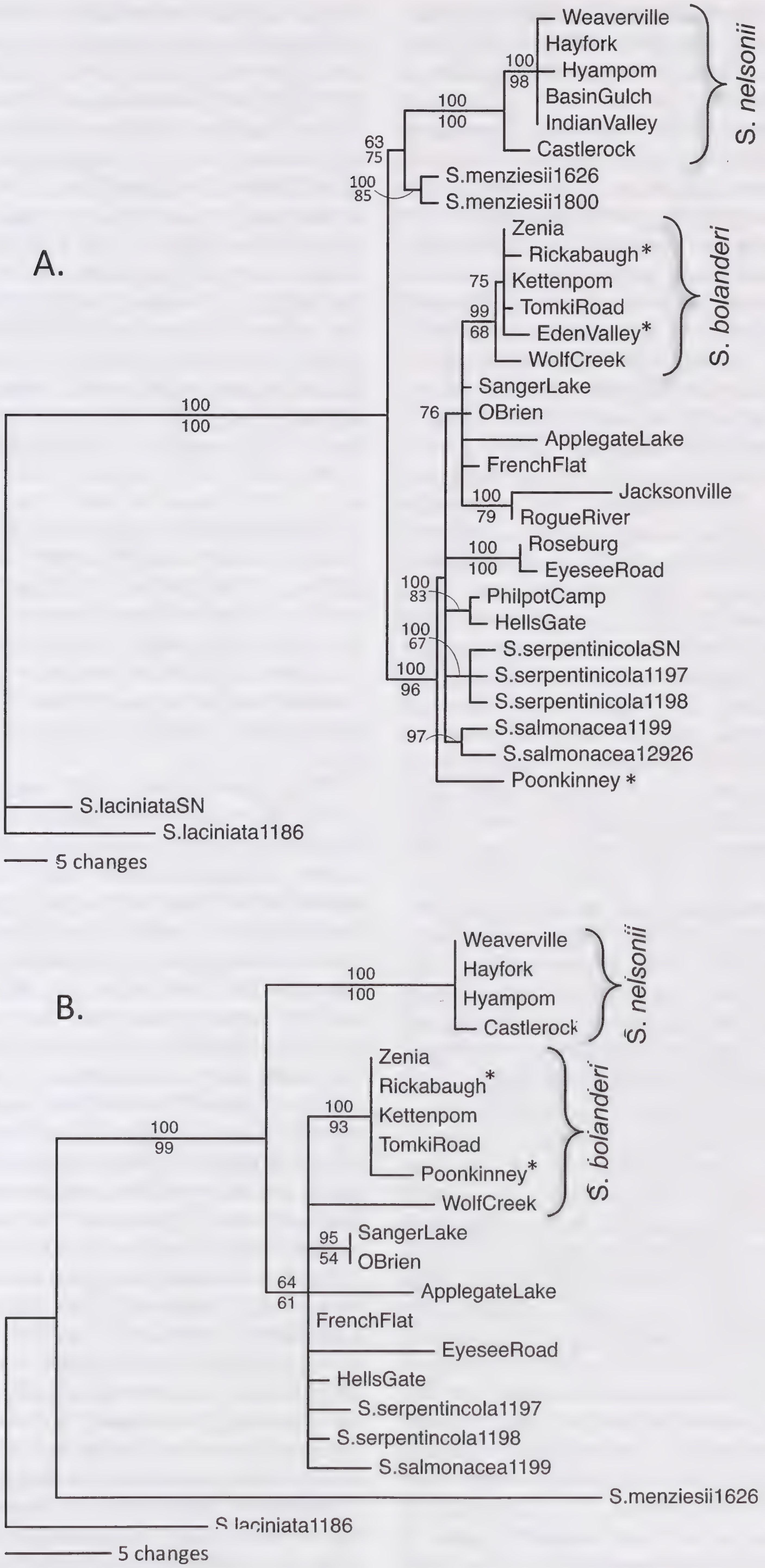

FIG. 8. Strict consensus tree of relationships among collections of *Silene* based on maximum parsimony analysis of (A) cpDNA sequence variation and (B) ITS region sequence variation. Location names outside of braces refer to *S. hookeri* collections; asterisks note morphologically ambiguous collections. Branch lengths are proportional to number of changes (substitutions and indels); if >50%, Bayesian posterior probability (upper) and bootstrap percentage (lower) accompany nodes. Three nodes on the cpDNA tree with low bootstrap support show Bayesian values only.

interpret. Critical differences that are readily apparent in the field (e.g., presence/absence of petal appendages, depth of petal lobing) are not always obvious in the herbarium.

We likewise believe that *S. bolanderi* should be treated as separate species, distinct from *S. hookeri*, but the application of the name *S. bolanderi* has a complicated history because previous authors who recognized the taxon (as a species or subspecies) appear to have confused it, at least partly, with *S. nelsonii*. For example, Hitchcock and Maguire's (1947) brief description of *S. hookeri* subsp. *bolanderi* is consistent with Gray's (1868) concept of *S. bolanderi*, but they cite two specimens of *S. nelsonii* as examples. The plants Nelson et al. (2006, Table 2) described as *S. bolanderi* and the ones that key to *S. hookeri* subsp. *bolanderi* in Morton (2005) are actually *S. nelsonii*. The description of *S. bolanderi* in Hartman et al. (2012) also matches *S. nelsonii*, with the exception of flower color and geographical range, which are given as white or pink and Outer North Coast Ranges (NCoRO), respectively. The flowers of *S. nelsonii* are never pink, and the species also occurs in the Klamath Region (KR). When properly circumscribed, *S. bolanderi* resembles *S. hookeri* in having pink petals with well-developed appendages, and in fact, the species has generally been treated as part of *S. hookeri* (Hooker 1873; Watson 1880; Gray 1878; Jepson 1925; Abrams 1944; Hitchcock and Maguire 1947; Munz and Keck 1959; Smith and Wheeler 1990–1991; Wilken 1993).

The case for recognizing *S. bolanderi* as a distinct species rests on a combination of morphological and molecular evidence. With only two exceptions, the differences between the *S. bolanderi* and *S. hookeri* populations we have seen in the field are obvious and striking, especially when two previously unappreciated traits – androecium symmetry and corolla form – are taken into account (Figs. 6, 7). In addition, all of the herbarium specimens of putative *S. bolanderi* we have examined from other sites in southern Humboldt and Trinity counties match the species based at least in flower size and petal lobe shape (other traits could not be scored reliably in all cases); the same is true for most historical collections from Mendocino County. Moreover, the California populations we sampled with unambiguous *S. bolanderi* morphology nest as part of a well-supported clade on both the cp and ITS trees. Placement of the Rickabaugh Glade population in this clade on both trees supports inclusion in *S. bolanderi* even though its flowers are smaller and less deeply lobed than other members of the species. In contrast, the apparent combination of *S. bolanderi*- and *S. hookeri*-like traits at Poonkinney Rd could indicate a history of hybridization between the two species, a hypothesis consistent with the incongruence of the cladogram topologies supported by cp and ITS sequences. The difficulty of interpreting herbarium specimens notwithstanding, a few other populations in eastern Mendocino and adjacent Lake counties (Fig. 3) appear intermediate between the two species and together may comprise a narrow hybrid zone (see Appendix 1 and label comments on *Bacigalupi 1526* [DS] and *Hamann and Dearing 113A* [JEPS]). The two species may have hybridized in northwestern Oregon as well. The single plant we sampled from Wolf Creek (Josephine Co., Oregon) combined the chloroplast nucleotide sequence of *S. bolanderi* and the ITS sequence of the *S. hookeri* + *S. bolanderi* clade, although the plants in this population closely resemble *S. bolanderi* from California. Establishing the role of historical hybridization, if any, will require additional data, but current opportunities for hybridization between *S. bolanderi* and *S. hookeri* appear quite limited. At least in California, the two species are separated geographically (Fig. 3; most populations of *S. hookeri* occur north of *S. bolanderi*). We know of only one area where they apparently occur together (Eden Valley, Mendocino County; Smith and Wheeler, 1990–1991), but it is unclear if they are truly sympatric there because the locality is currently inaccessible (J. Wheeler, Bureau of Land Management, personal communication). In sum, although closely related to *S. hookeri*, available evidence supports recognition of *S. bolanderi* as an independent, morphologically distinguishable lineage.

Popp and Oxelman (2007) showed that *S. hookeri* is an allohexaploid derivative of hybridization between parental species belonging to the predominantly tetraploid clade (*Physolychnis s.l.*) that includes most North American *Silene* and a smaller, mainly diploid clade that includes *S. menziesii*. Based on their morphological similarity to *S. hookeri*, we propose that *S. bolanderi*, *S. nelsonii*, *S. salmonacea*, and *S. serpentinicola* were derived from the same allopolyploidization event and, along with *S. hookeri*, comprise a monophyletic complex of related species (named for the first species described in the group). This hypothesis receives support from our ITS cladogram, which resolves a strongly supported clade including all five species and separate from *S. laciniata* and *S. menziesii*. In contrast, the cp tree suggests that *S. nelsonii* should be excluded from the *S. hookeri* complex; it appears as sister to *S. menziesii* in a weakly supported clade that is sister to a group including *S. bolanderi*, *S. hookeri*, *S. salmonacea*, and *S. serpentinicola*. This result was unexpected given the strong morphological difference between *S. menziesii* and *S. nelsonii*, but it may signify that *S. nelsonii*, like some *S. menziesii*, is diploid and, in fact, that it was one of the parents of the *S. hookeri* complex. At present, chromosome numbers are known only for *S. hookeri* and *S. serpentinicola*, both of which are hexaploids (Kruckeberg 1960; Chambers and Meyers 2011). Numbers for the other species (especially *S. nelsonii*), as well as a more robust phylogenetic analysis with broader taxon sampling and additional nuclear genes, will be needed to determine the composition of the *S. hookeri* complex.

Plants assignable to *S. hookeri* on morphological grounds do not comprise a monophyletic group on either the cp or ITS tree (Fig. 8). One plausible explanation is that as the species spread to occupy its current range in northwestern California and southwestern Oregon, it gave rise to *S. bolanderi*, *S. salmonacea*, and *S. serpentinicola*, but otherwise remained little changed, and thus represents a plesiospecies (Olmstead 1995). Additional evidence will be needed to evaluate this proposal, but at this point we strongly favor retaining *S. hookeri*, *S. salmonacea*, and *S. serpentinicola* as separate species. An alternative approach, which combines all of them along with *S. bolanderi* into a single species, would unite morphologically distinctive elements that are almost certainly reproductively isolated from one another.

Conservation implications. Our study along with previous work by Thomas Nelson and colleagues (Nelson and Nelson 2004; Nelson et al. 2006) interprets *S. hookeri sensu lato* as a complex of five closely related species, all of which are in varying degrees rare in California and worthy of conservation concern. Both *S. salmonacea* and *S. serpentinicola* are currently listed as California Rare Plant Rank 1B.2 species based on their restricted distributions and limited number of occurrences (CNPS 2019). *Silene nelsonii* is likewise a narrow endemic, restricted to an area of about 1600 km^2 in central Trinity and adjacent Humboldt and Shasta counties in the vicinity of the Trinity River and its tributaries (Fig. 4). We know of more than 70 occurrences (separated by at least 0.4 km), which vary in size from fewer than 10 to well over 100 plants. Populations occur in relatively mesic grassy openings in mixed conifer-hardwood forests, along roads, or on exposed dry rocky slopes. The main microsite requirement appears to be relatively deep soils, which are required to allow development of long taproots. Potential threats include soil disruption or removal caused by road maintenance and expansion, trampling by grazing cattle, and severe fires that kill taproots. The species appears to benefit from canopy removal and moderate soil disturbance caused by logging, perhaps by creating bare soil for recruitment, but intense site preparation, herbicide use, and repeated disturbance resulting from industrial forestry practices are significant threats (J. K. Nelson, personal communication). Since many populations are large and apparently healthy and most occur on relatively remote public lands managed by the Shasta-Trinity National Forest, we recommend a California Rare Plant Rank of 4.3 (Plants Rare or Endangered in California and elsewhere; not very threatened in California, <20% of occurrences threatened) (CNPS 2019).

Silene bolanderi is more widely distributed than *S. nelsonii* but likely more sensitive. The species ranges from Mendocino to southern Humboldt and Trinity counties in California (Fig. 3) and occurs as a cluster of disjunct populations in the northwestern corner of Josephine County, Oregon, where it is considered rare and "critically imperiled" (Oregon Biodiversity Information Center, 2019). Smith and Wheeler (1990–1991) regarded the species (referred to as *S. hookeri* subsp. *bolanderi*) as "locally common in northern Mendocino County" and J. P. Tracy noted on a specimen label (*18880*, UC1223229) that it was "frequent under oaks on Burr Valley Rd" (near Buck Mountain, Humboldt County), but our extensive field reconnaissance and conversations with expert regional botanists (G. Hulse-Stephens, C. Williams, T. Sholars) suggest that it may now be quite rare in California. Several historical collection sites occur on private lands that are no longer accessible, and a substantial area of potential suitable habitat remains unexplored across the range of the species. The number of extant California occurrences is uncertain, but likely quite small; we can confirm only 16. With the exception of newly discovered large populations near Zenia (Trinity County) and the large population at Rickabaugh Glade (Mendocino County), most of the known occurrences consist of 50 or fewer plants. Populations are vulnerable to ungulate grazing and trampling, road work, and conversion of habitat for high-value agriculture. We recommend a California Rare Plant Rank of 1B.2 (Plants Rare or Endangered in California and elsewhere; moderately threatened in California, 20–80% of occurrences threatened).

Silene hookeri is the most widely distributed species in the complex, with populations ranging from northwestern Mendocino County (single putative population at Eden Valley, *Wheeler 349*, BLMAR) through Humboldt, Trinity, Del Norte, and Siskiyou counties into western Oregon, where it is not considered rare (Fig. 3). In California, however, the species is known from only 18 scattered extant locations north of the Mendocino population, mainly in the Six Rivers, Siskiyou-Rogue, and Shasta-Trinity National Forests (Fig. 3). Additional exploration is warranted, but we recommend a rank of 2B.2 (Plants Rare or Endangered in California, but more common elsewhere, 20–80% of occurrences threatened) based on the limited number of occurrences and small size (<20 plants) of most of the populations.

Identification. The following key to members of the *S. hookeri* complex relies on floral traits and geography because we could not find vegetative or fruit differences that reliably separate the species. Identification of *S. salmonacea* and *S. serpentinicola* is straightforward based on obvious differences in petal color and geographical distribution (Nelson and Nelson 2004; Nelson et al. 2006). In contrast, identification of the other three species can be challenging because of substantial variation and overlap for generally useful traits like flower diameter, petal length, depth and equality of petal lobing, and expression of coronal petal appendages (Table

2). For example, *S. nelsonii* flowers are probably the largest among North American *Silene*, but flower diameter overlaps with *S. hookeri*, which has the smallest flowers in the complex. Overall corolla shape and androecium symmetry are more consistent, but are best evaluated before styles elongate because the petals spread apart and stamens change position as flowers age. Unfortunately, neither trait can be scored with certainty on herbarium specimens. The same is true for petal base vestiture, which is the single best way to recognize *S. nelsonii*. Some traits used in earlier treatments are problematic and not used here. For example, anther position, given as "included" for *S. hookeri* by some authors (Nelson and Nelson 2004; Nelson et al. 2006; Hartman et al. 2012), varies from slightly to distinctly exserted, and this character can be difficult to evaluate for taxa with broadly open corollas with poorly defined throats (*S. bolanderi, S. nelsonii, S. salmonacea*). Hairs on the upper stems and calyces of *S. hookeri* subsp. *hookeri* are usually non-glandular (cf. Hartman et al. 2012, page 619; cf. Hitchcock and Maguire 1947, p. 44), but this trait varies within and among populations. The same is true for *S. bolanderi*. *Silene serpentinicola* is a strict serpentinophile; the other four taxa occur both on and off serpentine (cf. Hartman et al. 2012). With the exception of *S. hookeri*, species in the complex have more-or-less restricted, non-overlapping ranges, making geography useful for identification (Fig. 3). Evidently species in the complex are seldom sympatric; we have visited only two sites where pairs occur together (*S. nelsonii* and *S. hookeri* at Philpot Campground, Trinity Co.; *S. hookeri* and *S. serpentincola* along French Hill Rd, Del Norte Co.). At both sites, we found a limited number of putative hybrid individuals with intermediate morphology and apparently aborted pollen.

KEY TO *SILENE HOOKERI* COMPLEX OF NORTHWESTERN CALIFORNIA AND WESTERN OREGON

Our couplet 2 represents a proposed revision of the key by Hartman et al. (2012), starting at their couplet 38.

1. Petal limb red; calyx often reddish, hairs glandular; Del Norte Co., southern Curry Co. . . . . *S. serpentinicola*

1′ Petal limb white, pink, or salmon-orange; calyx green or whitish green, hairs glandular or not

    2. Petal limb salmon-orange or pink (rarely white); petal appendages conspicuous, consistent in size and shape; petal limb not lobed to base at center, inner lobes oblong to linear, <10 times longer than wide; petal bases glabrous or nearly so, antisepalous filaments clearly visible in nectar windows (elliptical gaps between petal bases) with hand lens; calyx hairs glandular or not

        3. Petal limb salmon-orange, fading to pale red; center of flower (upper claw surface) bright to pale green; petal appendages short (<1 mm), tips sharp or blunt; calyx hairs not glandular; Trinity Co. north of Weaverville, within 8 km of Trinity Lake . . . . *S. salmonacea*

        3′ Petal limb pale to bright pink (rarely white); center of flower pink or white; petal appendages linear, >1 mm, tips rounded to acute; calyx hairs glandular or not

            4. Petal limb +/- perpendicular to claw as stamens dehisce, gen <15 mm, inner lobes gen oblong, gen <4× times longer than wide, apices rounded or blunt, outer lobes gen <6 mm; stamens gen clustered on one side of a narrow, well-defined throat (best evaluated after all 10 anthers have dehisced but before styles elongate); Humboldt, Mendocino [Eden Valley], Trinity, Siskiyou, Del Norte Cos., western Oregon . . . . *S. hookeri*

            4′ Petal limb held at +/- 45 degrees in early male phase, spreading (sometimes recurving) as styles elongate, gen >15 mm, inner lobes narrowly oblong to linear, gen >5× longer than wide, apices rounded to acute, outer lobes gen >10 mm; stamens +/- evenly positioned around broader, less distinct throat; mainly south of Hwy 36 in California (Mendocino, southern Humboldt and Trinity Cos.), northwestern Josephine Co. in Oregon . . . . *S. bolanderi*

    2′ Petal limb white; petal appendages absent or present as inconspicuous, weakly developed and variable short teeth; petal limb lobed to base, inner lobes linear, gen >10 times longer than wide; petal bases gen densely ciliate, antisepalous filaments gen obscured by hairs on petal margins; calyx hairs not glandular; Humboldt Co. (near Willow Creek), Shasta Co. (Harrison Gulch), Trinity Co. (mainly south of Hwy 299 and north of Hwy 36). . . . . *S. nelsonii*

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APPENDIX 1

ADDITIONAL SPECIMENS EXAMINED

Silene bolanderi

USA. CALIFORNIA. **Humboldt Co.:** *Anderson 5698* (HSC); *Constance 2612* (CAS, POM, RSA); *Eastwood 4799* (CAS); *Kildale 2204* (CAS); *Kildale 10845* (CAS); *Mesler 818* (HSC); *Mesler 825* (HSC); *Mesler 1633* (HSC); *Mesler 1649* (HSC); *Montalvo 493* (HSC); *Nelson 444* (HSC);

Nelson 1849 (HSC); *Nelson 5256* (HSC); *Parks 791* (CAS, UC); *Tracy 4234* (UC); *Tracy 16283* (JEPS, UC); *Tracy 18880* (UC); *Yates 5719* (UC). **Mendocino Co.**: *Baker 11502 a* (UC); *Balls 20756* (RSA); *Beane 2020* (CAS, UC); *Bolander 4696* (GH [G00037857], UC [8457], on-line images); *Davy 5096* (UC); *Ferris 11668* (CAS, UC); *Ferris 11675* (CAS, RSA); *Head s.n.* (CAS); *Hutchison 2432* (CAS, JEPS, RSA); *Jepson 1853* (JEPS); *Kellogg s.n.* (CAS); *Kelly s.n.* (CAS); *Mason 5273* (UC); *Mesler 1187* (HSC); *Nelson 815* (HSC); *Rattan s.n.* (CAS); *Smith 6405* (CAS); *Smith 6409* (CAS); *Wheeler 975* (CAS); **Trinity Co.:** *Hoover s.n.* (HSC); *Kellogg 86* (CAS); *Mesler 817* (HSC); *Mesler 854* (HSC); *Mesler 855* (HSC); *Mesler 1185* (HSC); *Mesler 1194* (HSC); *Mesler 1438* (HSC); *Nelson 5336* (HSC); OREGON. **Josephine Co.:** *Mesler 1183* (HSC).

Silene hookeri ssp. *hookeri*

USA. CALIFORNIA. **Del Norte Co.:** *Baker 816* (HSC); *Clifton 3171* (HSC); *Jimerson s.n.* (HSC); *Kildale 9950* (CAS); *Mesler 856* (HSC); *Mesler 1196* (HSC); *Mesler 1201* (HSC); *Mesler 1486* (HSC); *Muth 4411* (HSC); *Overton 4181* (HSC); *Renner 2884* (HSC); *Tracy 16197* (UC); *Tracy 17192* (UC); *Tracy 18910* (UC); *Van Deventer s.n.* (HSC); **Humboldt Co.:** *Chandler 1539* (UC); *Kildale 9137* (CAS); *Mesler 1188* (HSC103745); *Mesler 1482* (HSC); *Mesler 1674* (HSC); *Smith 9932* (HSC); *York 168* (HSC); **Mendocino Co.:** *Wheeler 349* (BLMAR); **Siskiyou Co.:** *Quick 59-08* (CAS); *Rattan s.n.* (CAS); *Thomas 4122* (CAS); *Tracy 16273* (UC);**Trinity Co.:** *Chin 60* (HSC); *Erwin 100* (HSC); *Erwin 101* (HSC); *Ferlatte 2080* (HSC); *Ferris 11690* (UC); *Howell 30366* (CAS); *Jepson 16648* (JEPS); *Mesler 1189* (HSC); *Mesler 1192* (HSC); *Mesler 1652* (HSC); *Mesler 1653* (HSC); *Mesler 1654* (HSC); *Miller 12* (HSC); *Sharsmith 4372* (UC); *Sieburth 10* (HSC). OREGON. **Benton Co.:** *Hansen s.n.* (CAS); *Johnston (CAS); Maw s.n.* (UC); *Nelson 74* (CAS); **Douglas Co.:** *Abrams 10504* (CAS); *Gale 53* (CAS); *Gale 192* (CAS); *Henderson 12674* (UC); *Kimber s.n.* (CAS); *Mesler 1184* (HSC); *Roantree s.n.* (CAS); *Thompson 4393* (CAS); *Thompson 4403* (CAS); *Thompson 10156* (CAS); *Thompson 10192* (CAS); *Wiley s.n.* (JEPS); **Jackson Co.:** *Applegate 4220* (CAS); *Constance 2939* (HSC); *Henderson 5895* (CAS); *Mesler 1179* (HSC); **Josesphine Co.:** *Abrams 10356* (CAS); *Ackerman 246* (HSC); *Applegate 5040* (CAS); *Applegate 7299* (CAS); *Breedlove 3229* (CAS); *Dale s.n.* (CAS); *Eastwood 1358* (CAS); *Gale 7* (CAS); *Gale 21* (CAS); *Gale 208* (CAS); *Gale 233* (CAS); *Goff 108* (CAS, UC); *Gould 798* (UC); *Gould 1057* (UC); *Heller 10039* (CAS); *Henderson 95* (CAS, JEPS); *Hitchcock 19104* (UC); *Howell s.n.* (CAS); *Jimerson s.n.* (HSC); *Kelly 270* (HSC); *Kildale 7911* (CAS); *Kildale 9637* (CAS); *Mesler 1178* (HSC); *Mesler 1182* (HSC); *Weiler 61191* (UC); *Olmstead 98-24* (CAS); *Prescott s.n.* (CAS); *Renner 2861* (HSC); *Ripley 9594* (CAS); *Van Deventer s.n.* (HSC); **Lane Co.:** *Baker 2769* (UC); *Constance s.n.* (CAS); *Peck 22076* (CAS, UC); **Marion Co.**: *Gale 214* (CAS); **Yamhill Co.**: *Gardiner s.n.* (Kew, K00728878).

Silene nelsonii

USA. CALIFORNIA. **Humboldt Co.:** *Abrams 7114* (CAS); *Baker 2430* (HSC); *McRae s.n.* (HSC); *Newton 117* (HSC); *Spjut 1875* (HSC); *Tracy 5999* (UC); **Shasta Co.:** *Alcasas 91* (HSC); **Trinity Co.:** *Anderson 2455* (HSC); *Baker 2311* (HSC); *Baker 2326* (HSC); *Barneby 11551* (CAS); *Ferlatte 2071* (HSC); *Ferris 11688* (CAS, UC); *Goodyear s.n.* (CHSC); *Harris s.n.* (HSC); *Holman s.n.* (UC); *Junkans s.n.* (CAS); *Kildale 10816* (CAS); *Linstedt 25* (HSC); *Mesler 844* (HSC); *Mesler 847* (HSC); *Mesler 849* (HSC); *Mesler 851* (HSC); *Mesler 1477* (HSC); *Mesler 1484* (HSC); *Mesler 1641* (HSC103776); *Mesler 1668* (HSC); *Mesler 1672* (HSC); *Mesler 1673* (HSC); *Mesler 1690* (HSC); *Montalvo 257* (HSC); *Nelson 4684* (HSC); *Nelson 5175* (HSC); *Nelson 5372* (CHSC); *Nelson 5372* (HSC); *Nelson 5394* (HSC); *Nelson 5609* (HSC); *Nelson 9121* (HSC); *Newton 610* (HSC); *Oxner 25* (HSC); *Sharsmith 4359* (UC); *Smith 8191* (HSC); *Specht 191* (HSC); *Spellenberg 167* (HSC); *Tate 1416* (HSC); *Tate 1445* (HSC); *Taylor 1064* (CAS); *Taylor 2917* (CHSC); *Wilson s.n.* (UC); *York 3210* (HSC).

Silene salmonacea

USA. CALIFORNIA. **Trinity Co.:** *Cantelow 1246* (CAS); *Cantelow s.n.* (CAS); *Dayton 369* (CAS); *Eastwood 4947* (CAS); *Hoffman 2446* (UC); *Janeway 5024* (CHSC); *McClintock s.n.* (CAS); *Nelson 9218* (HSC); *Smith 12926* (HSC); *Taylor 18097* (HSC); *True 761* (UC); *Yates 349* (UC).

Silene serpentinicola

USA. CALIFORNIA. **Del Norte Co.:** *Baker 1733* (HSC); *Barker 643* (HSC); *Barker 1611* (HSC); *Carothers s.n.* (HSC); *Clifton 2560* (HSC); *Clifton 3322* (HSC); *Clifton 3365* (HSC); *Clifton 5334* (HSC); *Clifton 5397* (HSC); *Clifton 7589* (HSC); *Deventer s.n.* (HSC); *Harris s.n.* (HSC); *Hoover s.n.* (HSC); *Imper 1422* (HSC); *Imper 1425* (HSC); *Imper s.n.* (HSC); *Jimerson s.n.* (CAS); *Jimerson s.n.* (HSC); *McRae 208* (HSC); *Mesler 1462* (HSC); *Mesler 1463* (HSC); *Mesler 1485* (HSC); *Mesler 1486* (HSC); *Mesler 1487* (HSC); *Nelson 4151* (HSC); *Nelson 4151* (HSC); *Nelson 4164* (HSC); *Nelson 4164* (HSC); *Nelson 8736* (HSC); *Nelson 8981* (HSC); *Nelson 9085* (HSC); *Nelson 9175* (HSC); *Renner 582* (HSC); *Renner 611* (HSC); *Renner 626* (HSC); *Renner 2844* (HSC); *Renner 2848* (HSC); *Renner 2850* (HSC6); *Renner 2852* (HSC); *Renner 2868* (HSC); *Renner 2897* (HSC); *Renner 2901* (HSC); *Renner 2904* (HSC); *Renner 2908* (HSC); *Renner 2909* (HSC); *Renner 2912* (HSC); *Renner 2928* (HSC); *Renner 2932* (HSC); *Smith 6718* (HSC); *York 906* (HSC).

Species identification uncertain

USA. CALIFORNIA. **Lake Co.:** *Hamann 1113A* (JEPS); *Howe 3091* (SDSU); *Lodge 378* (UC); **Mendocino Co.:** *Bacigalupi 1526* (CAS); *Eastwood 15200* (CAS); *Janeway 10474* (CHSC, on-line image); *Jones 3814* (CAS); *Nelson 9118* (HSC); *Smith 2354* (CAS); *Smith 6443* (CAS); *Wayman* 283 (HSC); *Wiggins 12150* (CAS, UC).

APPENDIX 2
GENBANK ACCESSION NUMBERS
SIBO = *S. bolanderi*; SIHO = *S. hookeri* ssp. *hookeri*; SIHOPU = *S. hookeri* ssp. *pulverulenta*; SILA = *S. laciniata*; SINE = *S. nelsonii*; SISA = *S. salmonacea*; SISE = *S. serpentinicola*; UNC = species identification uncertain. All vouchers held at HSC.

Locality	Taxon	State: county	Collection	*trnH*	*trnQ*	*rpL16*	*rpS16*	*ITS*
Kettenpom	SIBO	CA: Trinity	Mesler (855)	MN231096	MN231128	MN231159	MN231191	MN231221
Rickabaugh	SIBO	CA: Mendocino	Mesler (1185)	MN231095	MN231127	MN231158	MN231190	MN231220
Tomki Road	SIBO	CA: Mendocino	Mesler (1187)	MN231098	MN231130	MN231161	MN231193	MN231223
Wolf Creek	SIBO	OR: Josephine	Mesler (1183B)	MN231097	MN231129	MN231160	MN231192	MN231222
Zenia	SIBO	CA: Trinity	Mesler (854)	MN231094	MN231126	MN231157	MN231189	MN231219
Applegate Lake	SIHO	OR: Jackson	Mesler (1179)	MN231102	MN231134	MN231165	MN231197	MN231227
Orleans	SIHO	CA: Humboldt	Mesler (1188)	MN231105	MN231137	MN231168	MN231200	MN231229
French Flat	SIHO	OR: Josephine	Mesler (1182)	MN231103	MN231135	MN231166	MN231198	MN231228
Roseburg	SIHO	OR: Douglas	Mesler (1183A)	MN231104	MN231136	MN231167	MN231199	—
Hell's Gate	SIHO	CA: Trinity	Mesler (1192)	MN231107	MN231139	MN231170	MN231202	MN231230
O'Brien	SIHO	OR: Josephine	Mesler (1178)	MN231101	MN231133	MN231164	MN231196	MN231226
Philpot Camp	SIHO	CA: Trinity	Mesler (1189)	MN231106	MN231138	MN231169	MN231201	—
Sanger Lake	SIHO	CA: Del Norte	Mesler (856)	MN231100	MN231132	MN231163	MN231195	MN231225
Jacksonville	SIHOPU	OR: Jackson	Mesler (1180)	MN231109	MN231141	MN231172	MN231204	—
Rogue River	SIHOPU	OR: Jackson	Mesler (1181)	MN231110	MN231142	MN231173	MN231205	—
Cow Mtn	SILA	CA: Mendocino	Mesler (1186)	MN231119	—	MN231182	MN231214	MN231235
Weitchpec	SILA	CA: Humboldt	MacIntosh (s.n.)	MN231118	MN231150	MN231181	MN231213	—
Silver Lake	SIME	CA: Lassen	Mesler (1626)	MN231116	MN231148	MN231179	MN231211	MN231234
Deer Creek	SIME	CO: Jefferson	Wittmann (1800)	MN231117	MN231149	MN231180	MN231212	—
Basin Gulch	SINE	CA: Shasta	Mesler (1476)	MN231091	MN231123	MN231154	MN231186	—
Castlerock	SINE	CA: Trinity	Mesler (1481)	MN231092	MN231124	MN231155	MN231187	MN231218
Hayfork	SINE	CA: Trinity	Mesler (844)	MN231089	MN231121	MN231152	MN231184	MN231216
Hyampom	SINE	CA: Trinity	Mesler (849)	MN231090	MN231122	MN231153	MN231185	MN231217
Indian Valley	SINE	CA: Trinity	Mesler(1484)	MN231093	MN231125	MN231156	MN231188	—
Weaverville	SINE	CA: Trinity	Mesler (821)	MN231088	MN231120	MN231151	MN231183	MN231215
Trinity Center	SISA	CA: Trinity	Smith (12926)	MN231115	MN231147	MN231178	MN231210	—
Trinity Dam	SISA	CA: Trinity	Mesler (1199)	MN231114	MN231146	MN231177	MN231209	MN231233
Humboldt Flat	SISE	CA: Del Norte	Mesler(1197)	MN231112	MN231144	MN231175	MN231207	MN231231
Gasquet Mtn	SISE	CA: Del Norte	Mesler (1198)	MN231113	MN231145	MN231176	MN231208	MN231232
French Hill	SISE	CA: Del Norte	Mesler (sn)	MN231111	MN231143	MN231174	MN231206	
Eden Valley	UNC	CA: Mendocino	Nelson (9118)	MN231108	MN231140	MN231171	MN231203	
Poonkinney	UNC	CA: Mendocino	Wayman (283)	MN231099	MN231131	MN231162	MN231194	MN231224

MADROÑO, Vol. 66, No. 4, p. 194, 2019

ANNOUNCEMENT

2020 CBS BANQUET AT UC SANTA CRUZ

Save the Date! The 2020 Annual Banquet & Mixer of the California Botanical Society will be held at the UC Santa Cruz Arboretum and Botanic Garden on Saturday, April 4, 2020. The CBS Council is delighted to report that Dr. Kathleen Kay (Department of Ecology and Evolutionary Biology, UC Santa Cruz) will be delivering the evening's presentation. Details regarding the banquet's time and location, the title of Dr. Kay's talk, registration and payment, and recommendations for camping/lodging will be announced on the CBS website early in 2020.

Field trips will also be offered during the weekend of the banquet. If you are interested in leading a field trip, please send a description of your prospective trip (including the maximum number of participants) to our local organizer, Brett Hall (brett@ucsc.edu).

—SUSAN J. MAZER, President, California Botanical Society, Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, 93106, mazer@lifesci.ucsb.edu.

Madroño, Vol. 66, No. 4, pp. 195–196, 2019

CBS PRESIDENT'S REPORT FOR VOLUME 66

Dear Colleagues,

Every summer, I'm called upon to reflect on the past year of Society activities, events, and milestones, most of which rest predictably within the annual or semi-annual cycle comprised of student research awards, recruitment of new members, mixers, banquet, graduate symposium, and welcoming of new Council members. All of these categories offer happy news this year.

Most recently, in June we announced the winners of the Paul Silva Student Research Grants. The 11 proposals that were submitted were so strong that the Council wrestled mightily to select the awardees. Our aim was to offer two awards, but in the end, we awarded four grants. This year's winners will examine compelling ecological patterns and processes or explore botanical diversity in regional hotspots. I was a particularly heartened by the many proposals for research that combine fieldwork with the testing of key ecological hypotheses or predictions.

For example, Lacey Benson, a Master's student at San Jose State University (advised by Dr. Susan Lambrecht), will investigate adaptation to drought in the western sword fern (*Polystichum munitum*). Her research takes a landscape-level approach to study geographic variation in the physiological and morphological traits of this fern's gametophytes, with the goals of linking desiccation tolerance, morphology, and historical exposure to drought in this highly vulnerable life stage. After collecting fertile fronds from populations along a north-south gradient ranging from Prairie Creek Redwoods State Park in Orick to Landels-Hill Big Creek Reserve in Big Sur, Lacey will cultivate gametophytes that she will then expose to cycles of drought and moisture, enabling her to examine biogeographic patterns with respect to the post-desiccation recovery rates and surface morphology of these gametophytes. Lacey's work holds the promise of helping us to understand the ecological limits and microhabitat requirements of ferns, and to recognize the complex ways in which these water-dependent taxa successfully occupy highly heterogeneous forests. Lacey's upcoming discoveries of gametophytes' adaptations to drought will help botany instructors everywhere demonstrate that there's much more to fern gametophytes than just being "heart-shaped"!

Alec Chiono, a Master's student at the University of San Francisco (advised by Dr. John Paul) will use his award to investigate differences in thermal niche breadth between coastal and inland populations of (the iconic and beautiful) *Erythranthe guttata* (aka *Mimulus guttatus*). Alec will employ a combination of growth chamber observations and ecological niche modeling to test the hypothesis that populations adapted to chronically variable conditions (i.e., inland populations) will be better able to withstand the effects of upcoming climate change than those historically exposed to more constant climatic conditions. Demonstrating the elevated vulnerability of coastal wildflowers to climate change relative to their inland counterparts would represent an important and wide-ranging contribution to our understanding of the abiotic effects of climate warming on the California flora.

Christina Varnava, a Master's student at Claremont Graduate University and Rancho Santa Ana Botanic Garden (advised by Dr. J. Travis Columbus), will create a vascular flora of the Upper Sespe Creek Watershed, one of the unsung "black holes" of the Los Padres National Forest (in northern Ventura County) that is in urgent need of a comprehensive floristic inventory. While this watershed has been previously surveyed and sampled, most herbarium specimens from the region represent roadside collections. Accordingly, Christina will focus on the unexplored tributaries and undocumented grasslands. In addition, given the 2017 Thomas Fire's effects on the southern portion of the Upper Sespe Creek Watershed, Christina's inventory will contribute to our understanding of the effects of intense wildfires on the recovery of natives and the opportunities for invasive species to spread. The importance of new and significant collections of vouchered specimens for studies of plant phenology, biogeography, and range extensions of both rare and common species also makes Christina's project highly noteworthy.

In further support of floristic research, Maria Jesus — also a Master's student at Claremont Graduate University and Rancho Santa Ana Botanic Garden (advised by Dr. Naomi Fraga) — was granted an award to create a vascular flora of Conglomerate Mesa and Malpais Mesa in Inyo County. While meritorious in its own right as an investigation of floristic diversity, Maria's work is all the more urgent due to the fact that this region is under threat by exploratory gold-mining. Two floristic provinces (the Mojave Desert and Great Basin Desert) meet in this region as well, making it a unique and ecologically important flora in need of a baseline, and well-vouchered, floristic inventory. Maria's project will provide conservation advocates with a crucial tool with which to track and protect this region's endemic species. To learn more about these researcher's projects, please read their abstracts posted on the CBS webpage.

Additional evidence that the next generation of western U.S. botanists is poised to do creative and outstanding work was on display at this year's Graduate Student Symposium — the 27th such event — held at California Polytechnic University, San Luis Obispo from April 5–7, 2019 along with pre- and post-symposium field trips. In part due to its accessibility from both northern and southern California, and in part due to the stellar organizational efforts of three faculty members — Drs. Jenn Yost, Dena Grossenbacher, and Matt Ritter — as well as the tireless assistance of graduate student Dena Paolilli, the meeting was very well attended by students from all over California and beyond. If you're a faculty member seeking REU students, Master's or Ph.D. students, or postdocs who are familiar with the California flora and are already accomplished public speakers, attending the CBS Graduate Student Symposium is a great way to meet splendid candidates.

High points of the symposium (in addition to the uniformly high spirits, ample time for conversation, 160 registered attendees, 37 oral presentations, and 33 posters) were the field trips to the Serpentine Irish Hills, to Shell Creek, and to Poly Canyon at peak wildflower season; the annual banquet and the keynote address by Dr. David Lowry (now at Michigan State University), who treated us to an overview of genetic, ecological, and physiological variation among the yellow monkeyflowers of western North America; and, of course, the challenge of selecting the prize-winning talks from among so many engaging presentations. Prize winners this year were Natalie Love (University of California, Santa Barbara) for Best Overall Presentation; Emily Cox (UC Berkeley – undergraduate!) for Best Talk; and Erin Coltharp and Chloe Knowd (California Polytechnic State University, SLO), and Nancy Conejo (San Francisco State University) for joint winners of Best Posters. Because we were so impressed with the quality of presentations, we created an Honorable Mention category, in which we acknowledged the following: Ryan Buck (San Diego State University); Andy Siekkinen (Rancho Santa Ana Botanic Garden/Claremont Graduate University), and Dena Paolilli (California Polytechnic State University, SLO) for Honorable Mention Talks; and Drew Gilberti (California State University, Chico), and Vivian Avila and Elias Acosta-Mendosa (Santa Clara University) for their eye-catching posters.

One of the Society's most promising outreach activities in both 2018 and 2019 resulted from our presence at two large Science Fairs. Due to the joint work of *Madroño* Editor-in-Chief, Dr. Justen Whittall, and *Nemophila* editor, Josie Lesage, in March 2019 we presented awards to 13 students who individually and as teams represented nine botanical entries at the Synopsys Championship (Santa Clara County) and the Santa Cruz County Science & Engineering Fair. The excitement and smiles among the winners raises our hope that the availability of these awards will ignite and elevate interest in botanical research among budding (sorry about the pun) scientists ranging from elementary to high school students. And who *wouldn't* want to know whether plants absorb microplastics? If you'd like to serve as a judge in your county's Science Fairs, please contact Justen Whittall who can provide you with judging and awards materials on behalf of the California Botanical Society.

Looking towards the future, now is the time to start planning your attendance at the 2020 annual banquet (the next Graduate Symposium will be in 2021), which will be hosted by the Arboretum at the University of California, Santa Cruz. Brett Hall (California Native Plant Program Director) has graciously offered to organize this event, and I'm looking forward to wildflower-dominated field trips and time to explore the Arboretum. We plan to schedule plenty of time before the banquet for attendees to bring picnic lunches and to stroll around the Arboretum grounds. Please mark your calendars for this event; encourage your students, postdocs and colleagues to participate; and help them to arrange transportation to and from the Arboretum.

Finally, please talk with your students and colleagues about submitting their manuscripts to *Madroño* for publication, and if you're considering publishing in *Madroño* yourself, we're eager to receive your manuscripts. Our esteemed peer-reviewed quarterly journal offers color plates and open access with an average time from submission to print delivery of less than six months (available online sooner!).

This letter wouldn't be complete without pausing to acknowledge the tragedy that touched many California Botanical Society members last October: the murder of Jessica Orozco, a young botanist who completed her Master's degree in 2016 at Claremont Graduate University/Rancho Santa Ana Botanic Garden and had begun her career as a Range Land Specialist for the Hualapai Tribe in Kingman, Arizona. Jessica's fledgling career was the perfect match for her interests and expertise in rangeland monitoring, plant identification, land and livestock management, and working with Tribal communities. While the personal loss to her friends and family is incalculable, when such a bright, joyful, and high-spirited beacon is lost from our community at such a young age, I can't help but think of all of the people who Jessica had not yet met, but with whom she would have shared her unbridled enthusiasm and love of plants, particularly those for whom she would have been the one to provide an initial spark of botanical interest. It now falls on all of us to help to tend and fill the gap that Jessica's passing left behind. Please read more about Jessica's life and influence in the dedication of volume 66 in *Madroño* 66(1): 1–3.

Until our paths cross again, I hope you have a great winter and, if we haven't yet met, please introduce yourself to me at next year's annual banquet in Santa Cruz.

Susan Mazer

Susan J. Mazer
Professor of Ecology and Evolution
University of California, Santa Barbara
email: sjmazer@ucsb.edu

MADROÑO, Vol. 66, No. 4, pp. 197, 2019

EDITOR'S REPORT FOR VOLUME 66

I am pleased to report the publication of *Madroño* volume 66 by the California Botanical Society for 2019.

In my second year editing *Madroño* solo, I have attempted to keep *Madroño* on track and at the leading edge of peer reviewed, scientific publications in natural history. Highlights from this past year include publishing six full-length Contents articles, six formal Notes, nine Noteworthy Collections and four manuscripts describing New Species.

After last year's inaugural Open Access articles, we added several additional Open Access articles to the *Madroño* library including two in this very issue. Our contributions from graduate students continue to grow thanks to outreach efforts from the California Botanical Society Board and our membership. In particular, I'd like to point out Rancho San Ana Botanic Garden Ph.D. candidate Keir Morse's new species of *Malacothamnus* (issue #3) Nuri Benet-Pierce's thorough graduate studies of "narrow leaved" Chenopodiums with Michael Simpson (issue #2).

Administratively, we have instituted a flat rate for color figures with a wavier option for special circumstances. We are grateful for the efforts of 32 reviewers, several of which reviewed multiple contributions this past year. The list of reviewers found in this issue also includes numerous graduate students partaking in our reviewer-in-training program through California Botanical Society's outreach program (aka The Botany Ambassadors).

The average time from submission to publication for *Madroño* has dropped from eight months to less than seven months thanks to our reviewers and authors providing quick responses. We believe that *Madroño* is still the best outlet for western botanists to publish their discoveries in a timely fashion, while reaching a dedicated and passionate audience. We are always on the lookout for Special Issue topics and Guest Editors.

The efforts of numerous individuals are critical to the continued quality publication of Madroño. This year, I want to highlight the dedicated and detailed efforts of our Copy Editor, Dr. Alisa Hove. Although she no longer resides in the west (she is Professor at Warren Wilson College in North Carolina), her academic training (undergraduate at UC Davis, master's at Humboldt State, and Ph.D. at University of California Santa Barbara) provides the solid foundation for her careful copy editing that goes well beyond spelling and grammar. As always, I am grateful to our Noteworthy Collections editor, David Keil, our Book Editor, Matt Ritter, our Indexer extraordinaire, Steve Timbrook, and the administrative support provided by Lynn Yamashita and Rachael Olliff-Yang.

I find great pleasure in helping cultivate manuscripts from the submission process to the printed copy that arrives in our mailboxes. Being on the forefront of discoveries in western botany and working with such astute and passionate authors and reviewers is a pleasure. Botany is alive and well in western North America! The evidence is in *Madroño*. Please continue to submit your work to the journal, recruit new authors, and have a great year.

Justen Whittall
November 2019

Madroño, Vol. 66, No. 4, pp. 198, 2019

REVIEWERS OF MADROÑO MANUSCRIPTS 2019

Alexander P. Sukhorukov
Andrew Salywon
Barbara Mary Thiers
David Keil
Dean W Taylor
Ivalu Caucho
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Jason Singhurst
Jon Rebman
Katharine Cary
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Robert Preston
Sharon Strauss
Socorro González-Elizondo
Stephen Sillett
Sula Vanderplank

MADROÑO, Vol. 66, No. 4, pp. 199–200, 2019

INDEX TO VOLUME 66

Classified entries: Major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

Alaska: Noteworthy collections: *Carex echinata* subsp. *echinata, C. lapponica, C. phaeocephala, Draba aleutica, Eriophorum viridicarinatum, Limosella aquatica, Persicaria lapathifolia, Primula tschuktschorum, Gnaphalium uliginosum*, 125.
Alternanthera philoxeroides, noteworthy collection from CA, 4.
Amaranthaceae (see *Alternanthera*)
Anacardiaceae (see *Malosma*)
Apiaceae (see *Petroselinum*)
Arbutus xalapensis ecological characteristics and distribution of populations in central TX, 47.
Asteraceae (see *Carduus* and *Sonchus*)
  Noteworthy collections: *Gnaphalium uliginosum*, from AK, 127.

Blepharidachne kingii, noteworthy collection from CA, 39.
Blue oak woodland (see *Quercus*)
Brassicaceae (see *Draba* and *Streptanthus*)

Cactaeae (see *Cylindropuntia*)
Calflora: tools for the 21st century plant lover, 120.
California: California phenological collections network, 130; *Calycanthus occidentalis*, dispersal by yellowjackets (*Vespula*), 41; Consortium of California Herabaria, upcoming changes, 37; *Dicentra uniflora*, biology of an ephemeral geophyte in southernmost Cascade Range, 148; *Lythrum*, notes on and typification, 97; old growth characteristics on a coast redwood (*Sequoia sempervirens*), pygmy forest ecotone, 14; *Quercus douglasii*, tree mortality in Sequoia Natl. Park, 164.
  New taxa: ***C. aureum, C. brandgegeeae, C. eastwoodiae, C. howellii, C. lineatum, C. luteum, C. sandersii, C. simpsonii, C. twisselmannii, C. wahlii***, 66-71; ***Malacothamnus enigmaticus***, 113; ***Strepanthus anomalus***, 24; ***Silene nelsonii***, 176.
  Noteworthy collections: *Alternanthera philoxeroides*, 4; *Blepharidachne kingii, 39; Isoetes orcuttii, 85; Malosma laurina*, 8; *Streptanthus cordatus* var. *cordatus*, 10.
California Botanical Society Annual Banquet 2020, 194.
California Consortium of Herbaria, 130.
Calochortus nitidus, noteworthy collection from WA, 13.
Calycanthaceae (see *Calycanthus*)
Calycanthus occidentalis, dispersal by yellowjackets (*Vespula*), 41.
Carduus cinerius, invasive sp. new to No. Am., 142.
Carex echinata subsp. *echinata, C. lapponica, C. phaeocephala*, noteworthy collections from AK, 125.
Caryophyllaceae (see *Silene*)
Chenopodiaceae (see *Chenopodium*)
Chenopodium: *C. hians, C. incognitum*, and ten new taxa within the narrow-leaved *Chenopodium* group in western North America, 56.
  New taxa: ***C. aureum, C. brandgegeeae, C. eastwoodiae, C. howellii, C. lineatum, C. luteum, C. sandersii, C. simpsonii, C. twisselmannii, C. wahlii***, 66-71.
Cupressaceae (see Sequoia)
Cylindropuntia: *C. wolfii*, nomenclatural history, revised description, and distribution, 76.
  New taxa: ***C. acanthocarpa*** subsp. ***ramosa***, ***C. alcahes*** subsp. ***gigantensis***, ***C. alcahes*** subsp. **mcgillii**, ***C. gander*** supsp. ***catavinensis***, ***C. imbricata*** subsp. ***rosea***, ***C. imbricata*** subsp. ***spinosior***, ***C. imbricata*** subsp. ***spinotecta***, ***C. thurberi*** subsp. ***versicolor***, ***C. whipplei*** subsp. ***enodis***, 91-93.
Cyperaceae (see *Carex* and *Eriophorum*)

Dicentra uniflora, biology of an ephemeral geophyte in southernmost Cascade Range, CA, 148.
Draba aleutica, noteworthy collection from AK, 125.
Drought effects in blue oak woodland (see *Quercus*)
Dispersal (see *Calycanthus*)

Editor's Report for Vol. 66, 197.
Ericaceae (see *Arbutus*)
Eriophorum viridicarinatum, noteworthy collection from AK, 126.

Fagaceae (see *Quercus*)

Gnaphalium uliginosum, noteworthy collection from AK, 127.

Invasive spp. (see *Carduus* and *Lythrum*)
Ipomopsis: Reassessment and circumscription of I. *multiflora* and *I.* polyantha, 87.
  New taxa: ***I. polyantha, I. multiflora, I. multifolora*** subsp. ***multifolora, I. multiflora*** subsp. ***brachysiphon, I. multiflora*** susp. ***whitingii***, 88-89.
Isoetaceae (see *Isoetes*)
Isoetes orcuttii, noteworthy collection from CA, 85.

Keys: *Carduus* spp. in No. Am., 192; *Chenopodium* spp. of CA, 73.

Liliaceae (see *Calochortus*)
Limosella aquatica, noteworthy collection from AK, 126.
Lythraceae (see *Lythrum*)
Lythrum in CA, 97.
Typification: ***L. adsurgens***, ***L. sanfordii***, 101.

Malvaceae (see *Malacothamnus*)
Malacothamnus enigmaticus, rare new sp. from San Diego Co., CA, 103.
Malosma laurina, noteworthy collection from CA, 8.

Nevada (see *Pennisetum*)

Oregon: Noteworthy collections: *Petroselinum segetum, Tropaeolum majus, Valerianella dentata, V. eriocarpa*, 11.
Orozco, Jessica Mae, Vol. 66 dedicated to, 1.

Papaveraceae (see *Dicentra*)

Parnassius clodius, (see *Dicentra*)
Pennisetum ciliare, noteworthy collection from NV, 86.
Persicaria lapathifolia, noteworthy collection from AK, 128.
Petroselinum segetum, noteworthy collection from OR, 11.
Poaceae (see *Blepharidachne* and *Pennisetum*)
Podsols (see *Sequoia*)
Polemoniaceae (see *Ipomopsis*)
Polygonaceae (see *Persicaria*)
President's Report for Vol 66, 195.
Primula tschuktschorum, noteworthy collection from AK, 127.
Primulaceae (see *Primula*)
Pygmy forest (see *Sequoia*)

Quercus douglasii, tree mortality in Sequoia Natl. Park, CA, 164.

Reviewers for Vol. 66, 198.
Reviews: *Baja California Plant Field Guide, 3rd Ed.* by Jon Rebman and Norm Roberts, 33; *C. G. Pringle: Botanist, Traveler, and the "Flora of the Pacific" (1881-1884)* by L. Mauz, 30; *Search for Ancient Agave Cultivars Across the Desert Southwest* by Ron Parker 34; *California Plants: A Guide to Our Iconic Flora* by Matt Ritter, 35.

Scrophulariaceae (see *Limosella*)
Sequoia sempervirens, old growth characteristics on a coast redwood pygmy forest ecotone, 14.
Serpentine (see *Streptanthus anomalus*)
Silene nelsonii, new sp. from Trinity River area, CA, 176.
Sonchus tenerrimus in NA north of Mexico, 80.
Streptanthus:***S. anomalus***, new sp. from CA, 24; *S. cordatus* var. *cordatus*, noteworthy collection from CA, 10.

Texas (see *Arbutus*)
Trinity River, CA (see *Silene*)
Tropaeolaceae (see *Tropaeolum*)
Tropaeolum majus, noteworthy collection from OR, 11.

Valerianaceae (see *Valerianella*)
Valerianella dentata and *V. eriocarpa*, noteworthy collections from OR, 11.

Washington (see *Calochortus*)

MADROÑO, Vol. 66, No. 4, pp. 201–203, 2019

MADROÑO VOLUME 66
TABLE OF CONTENTS

Alexander, Jason A., Upcoming changes in the Consortium of California Herbaria 37
Alexander, Jason A., (see Yost, Jenn M., et al.)
Ampersee, Nicholas J. (see Das, Adrian J., et al.)
Arthur, Aaron (see Preston, Robert E., et al.)
Baker, Marc A., Clarification of the name *Cylindropuntia wolfii* (Cactaceae) and an account of the species 76
Baker, Marc A., et al., Nomenclatural changes in *Cylindropuntia* (Cactaceae) 92
Barrington, David (see Gilman, Art)
Barry, Teri (see Yost, Jenn M., et al.)
Beck, John J. (see Burge, Dylan O.)
Bencie, Robin (see Yost, Jenn M., et al.)
Benet-Pierce, Nuri, and Michael G. Simpson, The taxonomy of *Chenopodium hians*, *C. incognitum*, and ten new taxa within the narrow-leaved *Chenopodium* group in western North America, with special attention to California 56
Bernhardt, Elizabeth A. (see Das, Adrian J., et al.)
Black, Danielle, Robert Patterson, and V. Thomas Parker, Dedication of Volume 66 to Jessica Mae Orozco 1
Bowler, Peter (see Yost, Jenn M., et al.)
Brainerd, Richard E. (see Halse, Richard R.)
Burge, Dylan O., and John J. Beck, Dispersal of spicebush (*Calycanthus occidentalis*, Calycanthaeae) by yellow jackets (Genus *Vespula*: Hymenoptera) 41
Carothers, Sydney K. (see Mesler, Michael R., Michael S. Mayer, and Sydney K. Carothers)
Carter, Benjamin (see Yost, Jenn M., et al.)
Chester, Tom (see Morse, Keir)
Cloud-Hughes, Michelle A. (see Baker, Marc A., et al.)
Coombs, Eric (see Gaskin, John F., et al.)
Crowe, Rebecca E. (see Yost, Jenn M., et al.)
Darin, Gina M. Skurka (see Walden, Genevieve K., et al.)
Das, Adrian J., et al., Tree mortality in blue oak woodland during extreme drought in Sequoia National Park, California 164
Davis, Austin M., and O. W. Van Auken, Ecological characteristics and distribution of *Arbutus xalapensis* (Texas madrone populations in central Texas 47
Dean, Ellen (see Yost, Jenn M., et al.)
Der, Joshua (see Yost, Jenn M., et al.)
Embrey, Teague, noteworthy collection from Nevada 86
Ertter, Barbara, and David Gowen, Notes on *Lythrum* (Lythraceae) in California: *Lythrum junceum* as a new (but old) introduced species, typification of Greene's *Lythrum* types, and possible hybridization of *Lythrum* in California 97
Fisher, Kirsten (see Yost, Jenn M., et al.)
Flores-Renteria, Lluvia (see Yost, Jenn M., et al.)
Frost, Gerald V. (see Wells, Aaron F., et al.)
Gaskin, John F., et al., *Carduus cinereus* (Asteraceae) – new to North America 142
Gilbert, Edward (see Yost, Jenn M., et al.)
Gilman, Art, and David Barrington, Review of *C. G. Pringle: Botanist, Traveler, and the "Flora of the Pacific Slope" (1881-1884)* by L. Mauz 30
Goforth, Brett, Noteworthy collection from California 8
Gowen, David (see Ertter, Barbara)
Grewell, Brenda (see Walden, Genevieve K., et al.)
Guilliams, C. Matt (see Yost, Jenn M., et al.)
Haggerty, Patricia K. (see Das, Adrian J., et al.)
Hains, Layla Aerne (see Yost, Jenn M., et al.)
Hall, Brett, Review of *California Plants: A Guide to Our Iconic Flora* by Matt Ritter 35
Halse, Richard R., Richard E. Brainerd, and Donna M. E. Ware, Noteworthy collections from Oregon ... 11
Hatfield, Colleen (see Yost, Jenn M., et al.)
Hendrickson, Larry (see Yost, Jenn M., et al.)
Huggins, Tom (see Yost, Jenn M., et al.)
Ives, Susan L. (see Wells, Aaron F., et al.)
Janeway, Lawrence (see Yost, Jenn M., et al.)
Johnson, Erin K. (see Wells, Aaron F., et al.)
Keil, David J. (see Gaskin, John F., et al.)
Kelch, Dean G. (see Gaskin, John F., et al.)

Kratville, David (see Walden, Genevieve K., et al.)
Lambert, Zuhayl (see Russell, Will)
Lay, Christopher (see Yost, Jenn M., et al.)
Litt, Amy (see Yost, Jenn M., et al.)
Macander, Matthew J. (see Wells, Aaron F., et al.)
Mackey, Halkard E. (see Schlising, Robert A.)
Majure, Lucas C. (see Baker, Marc A., et al.)
Markos, Staci (see Yost, Jenn M., et al.)
Mauldin, Jared (see Walden, Genevieve K., et al.)
Mayer, Michael S. (see Mesler, Michael R., Michael S. Mayer, and Sydney K. Carothers)
Mazer, Susan J., CBS President's Report for Volume 66 195
Mazer, Susan J. (see Yost, Jenn M., et al.)
McCamish, Danny (see Yost, Jenn M., et al.)
McDade, Lucinda (see Yost, Jenn M., et al.)
Mesler, Michael (see Yost, Jenn M., et al.)
Mesler, Michael R., Michael S. Mayer, and Sydney K. Carothers, *Silene nelsonii*, a new large-flowered species from the Trinity River area of northwestern California, USA, and a re-evaluation of *S. bolanderi* Gray 176
Mischler, Brent (see Yost, Jenn M., et al.)
Morse, Keir, and Tom Chester, *Malacothamnus enigmaticus* (Malvaceae), a new rare species from the desert edge of the Peninsular Range in San Diego County, California 103
Munson, Bryan (see Rebman, Jon, et al.)
Nazaire, Mare (see Yost, Jenn M., et al.)
Nydick, Koren R. (see Das, Adrian J., et al.)
O'Brien, Jon (see Walden, Genevieve K., et al.)
O'Connor, Kimberly (see Rebman, Jon, et al.)
O'Donnell, Richard, Noteworthy collection from California 10
Olson, Clare, Noteworthy collections from California 39
O'Rear, Teejay (see Walden, Genevieve K., et al.)
Ougzin, Aicha (see Walden, Genevieve K., et al.)
Parker, V. Thomas (see Black, Danielle)
Patterson, Robert (see Black, Danielle)
Pearson, Katelin D. (see Yost, Jenn M., et al.)
Pfaff, Anne H. (see Das, Adrian J., et al.)
Porter, Mark (see Gaskin, John F., et al.)
Potter, Dan (see Yost, Jenn M., et al.)
Preston, Robert E., et al., A new jewelflower (*Streptanthus*: Brassicaceae) from Marin Co., CA, USA 24
Rebman, Jon (see Baker, Marc A., et al.)
Rebman, Jon (see Yost, Jenn M., et al.)
Rebman, Jon, et al., Noteworthy collection from California 85
Riser, James. P., II, Noteworthy collection from Washington 13
Rosengreen, Lars (see Yost, Jenn M., et al.)
Rundel, Philip (see Yost, Jenn M., et al.)
Russell, Will, Zuhayl Lambert, and Suzie Woolhouse, Old-growth characteristics on a coast redwood (*Sequoia sempervirens* (D. Don) Endl.) pygmy forest ecotone 14
Sanders, Andrew (see Yost, Jenn M., et al.)
Santore, Joey, Review of *Baja California Plant Field Guide, 3^{rd} ed.* by Jon Rebman and Norm Roberts ... 33
Santore, Joey, Review of *Chasing Centuries: The Search for Ancient Agave Cultivars Across the Desert Southwest* by Ron Parker 34
Schlising, Robert A., and Halkard E. Mackey, Jr., Biology of the ephemeral geophyte, steer's head (*Dicentra uniflora*, Papaveraceae) in the southernmost Cascade Range, Butte County, California 148
Schusteff, Aaron (see Preston, Robert E., et al.)
Seltmann, Katja C. (see Yost, Jenn M., et al.)
Simpson, Michael G. (see Benet-Pierce, Nuri)
Simpson, Michael G. (see Yost, Jenn M., et al.)
Smith, Doreen (see Preston, Robert E., et al.)
Stephenson, Nathan L. (see Das, Adrian J., et al.)
Strother, John L., *Sonchus tenerrimus* (Asteraceae) in North America north of Mexico 80
Susanna, Alfonso (see Gaskin, John F., et al.)
Swiecki, Tedmond J. (see Das, Adrian J., et al.)
Van Auken, O. W. (see Davis, Austin M.)
Van Susteren, Jane (see Walden, Genevieve K., et al.)
Vanderplank, Sula (see Rebman, Jon, et al.)
Wahlert, Gregory A. (see Yost, Jenn M., et al.)
Walden, Genevieve K., et al., Noteworthy collection from California 4

Ware, Donna M. E. (see Halse, Richard R.)
Waselkov, Katherine (see Yost, Jenn M., et al.)
Wells, Aaron F., et al., Noteworthy collections from Alaska 125
Whittall, Justen, Editor's Report for Volume 66 197
Wilken, Dieter, Reassessment and circumscription of *Ipomopsis multiflora* and *Ipomopsis polyantha* (Polemoniaceae) 87
Williams, Kimberlyn (see Yost, Jenn M., et al.)
Wilson, Paul S. (see Yost, Jenn M., et al.)
Woods, Patrick W. (see Walden, Genevieve K., et al.)
Woolhouse, Suzie (see Russell, Will)
Yost, Jenn M., et al., The California phenology collections network: using digital images to investigate phenological change in a biodiversity hotspot 130

DATES OF PUBLICATION OF MADROÑO, VOLUME 66

Number 1, pages 1–38, published 10 June 2019
Number 2, pages 39–84, published 9 August 2019
Number 3, pages 85–124, published 11 October 2019
Number 4, pages 125–204, published 28 January 2020

Kruschke, David (see Walden, Genevieve K., et al.)
Lambert, Zabayl (see Russell, Will)
Lay, Christopher (see Yost, Jenn M., et al.)
Lin, Amy (see Yost, Jenn M., et al.)
Macander, Matthew J. (see Wells, Aaron F., et al.)
Mackey, Hallard E. (see Schlising, Robert A.)
Majure, Lucas C. (see Baker, Marc A., et al.)
Markos, Staci (see Yost, Jenn M., et al.)
Mauldin, Jared (see Walden, Genevieve K., et al.)
Mayer, Michael S. (see Mesler, Michael R., Michael S. Mayer, and Sydney K. Carothers)
Mazer, Susan J., [illegible]
Mazer, Susan J. (see Yost, Jenn M., et al.)
McCamish, Danny (see Yost, Jenn M., et al.)
McDade, Lucinda (see Yost, Jenn M., et al.)
Mesler, Michael (see Yost, Jenn M., et al.)
Mesler, Michael R., Michael S. Mayer, and Sydney K. Carothers. *Silene* [illegible], a new large-flowered species from the Trinity River area of northwestern California, USA, and a re-evaluation of *S. bolanderi* Gray 176
Mishler, Brent (see Yost, Jenn M., et al.)
Morse, Keir, and Tom Chester. *Malacothamnus enigmaticus* (Malvaceae), a new rare species from the desert edge of the Peninsular Range in San Diego County, California 103
Munson, Bryan (see Rebman, Jon, et al.)
Nazaire, Mare (see Yost, Jenn M., et al.)
Nydick, Koren R. (see Das, Adrian J., et al.)
O'Brien, Jon (see Walden, Genevieve K., et al.)
O'Connor, Kimberly (see Rebman, Jon, et al.)
O'Donnell, Richard. Noteworthy collection from California 10
Olson, Clare. Noteworthy collections from California 30
O'Rear, Tucker (see Walden, Genevieve K., et al.)
Ougzin, Aicha (see Walden, Genevieve K., et al.)
Parker, V. Thomas (see Black, Danielle)
Patterson, Robert (see Black, Danielle)
Pearson, Katelin D. (see Yost, Jenn M., et al.)
Pfaff, Anne H. (see Das, Adrian J., et al.)
Porter, Mark (see Gaskin, John F., et al.)
Potter, Dan (see Yost, Jenn M., et al.)
Preston, Robert E., et al. A new jewelflower (*Streptanthus*, Brassicaceae) from Marin Co., CA, USA 24
Rebman, Jon (see Baker, Marc A., et al.)
Rebman, Jon (see Yost, Jenn M., et al.)
Rebman, Jon, et al. Noteworthy collection from California 35
Riser, James P., II. Noteworthy collection from Washington 13
Rosengreen, Lars (see Yost, Jenn M., et al.)
Rundel, Philip (see Yost, Jenn M., et al.)
Russell, Will, Zabayl Lambert, and Susie Woolhouse. Old-growth characteristics on a coast redwood (*Sequoia sempervirens* (D. Don) Endl.) pygmy forest ecotone 14
Sanders, Andrew (see Yost, Jenn M., et al.)
Santore, Joey. Review of *Baja California Plant Field Guide, 3rd ed.* by Jon Rebman and Norm Roberts 53
Santore, Joey. Review of *Chasing Centuries: The Search for Ancient Agave Cultivars Across the Desert Southwest* by Ron Parker 34
Schlising, Robert A., and Hallard E. Mackey, Jr. Biology of the ephemeral geophyte, steer's head (*Dicentra uniflora*, Papaveraceae) in the southernmost Cascade Range, Butte County, California 185
Schusteff, Aaron (see Preston, Robert E., et al.)
Seltmann, Katja C. (see Yost, Jenn M., et al.)
Simpson, Michael G. (see Benet-Pierce, Nuri)
Simpson, Michael G. (see Yost, Jenn M., et al.)
Smith, Doreen (see Preston, Robert E., et al.)
Stephenson, Nathan L. (see Das, Adrian J., et al.)
Strother, John L. *[illegible]* (Asteraceae) in North America north of Mexico 80
Sustaita, Alfonso (see Gaskin, John F., et al.)
Swiecki, Tedmund J. (see Davis, Austin M.)
Van Auken, O. W. (see Davis, Austin M.)
Van Susteren, Jane (see Walden, Genevieve K., et al.)
Vanderplank, Sula (see Rebman, Jon, et al.)
Walden, Gregory A. (see Yost, Jenn M., et al.)
Walden, Genevieve K., et al. Noteworthy collections from California 4

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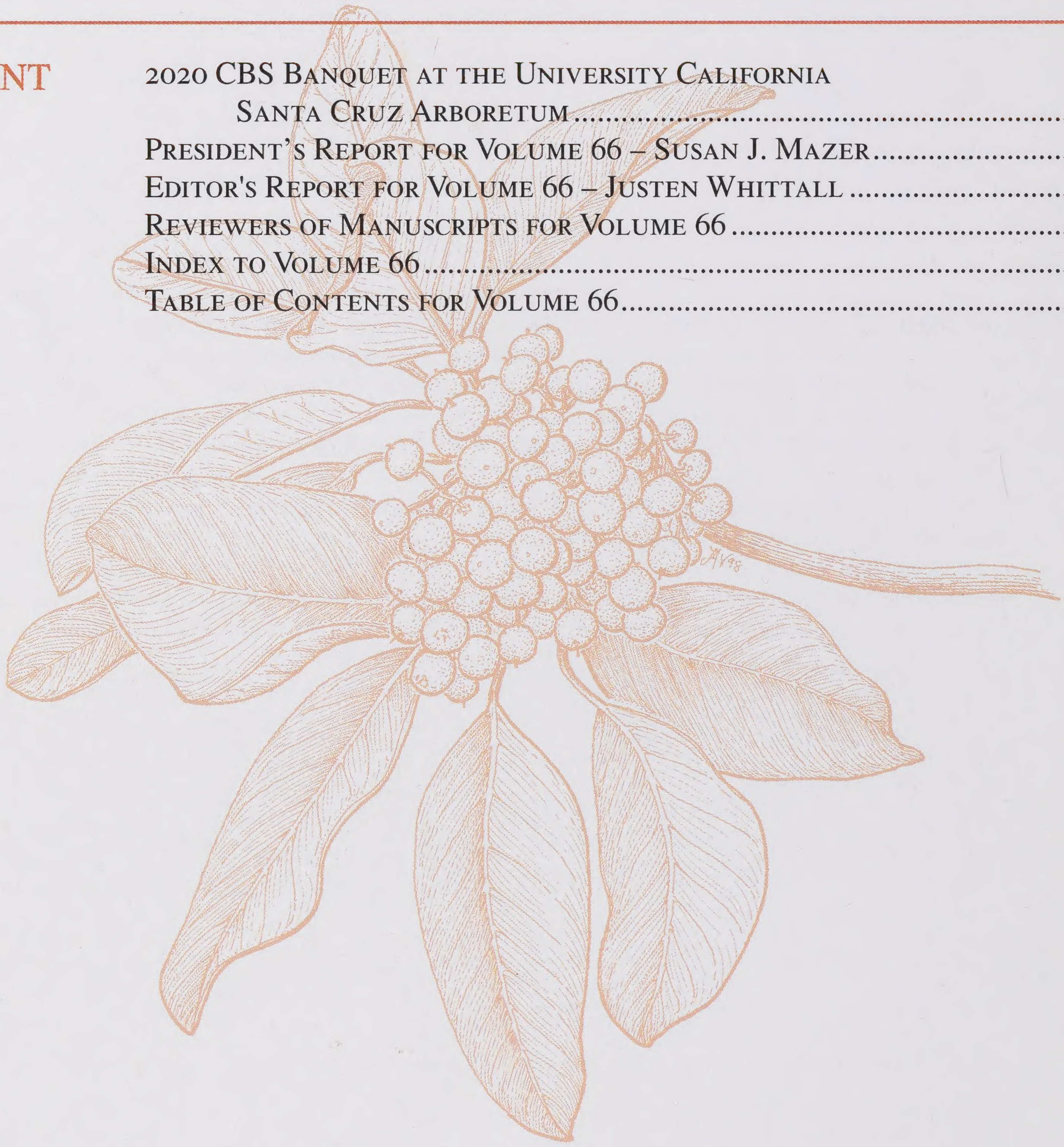
ANNOUNCEMENT

2020 CBS BANQUET AT THE UNIVERSITY CALIFORNIA SANTA CRUZ ARBORETUM 194
PRESIDENT'S REPORT FOR VOLUME 66 – SUSAN J. MAZER 195
EDITOR'S REPORT FOR VOLUME 66 – JUSTEN WHITTALL 197
REVIEWERS OF MANUSCRIPTS FOR VOLUME 66 198
INDEX TO VOLUME 66 199
TABLE OF CONTENTS FOR VOLUME 66 201



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